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THE FOOD OF INSECTS VIEWED FROM THE BIOLOGICAL AND HUMAN STANDPOINT [1]

By Charles T. Brues

Our present-day views concerning human food and nutrition are in such a state of active revolution, that it may seem futile to discuss the food of insects on the basis of the fragmentary knowledge we possess concerning these small animals. I have avoided the term nutrition, however, since food relates to actual materials and does not necessarily introduce chemical and physiological connotations. It is, therefore, clear that "entomological chop suey" might more adequately, if less elegantly, express the content of my subject matter, provided, of course, that we first separate and accurately identify all the disguised components of this delicacy. This separation, and identification of insect foodstuffs has, as a matter of fact, been rather thoroughly done by entomologists and affords the basis for an understanding of at least some of the principles that underlie the trophic behavior of insects.

That these peculiarities have determined to a great extent the evolution and differentiation of insects is very clear, and as I hope to indicate later we must also attribute to them a very important role among the many factors that have directed the course of organic evolution since the time when insects became a dominant figure in the living world.

The most striking feature of the diet of insects is the high degree of specificity which exists in the selection of

[1]Presented by the retiring president at the annual meeting of the Entomological Society of America at Des Moines, Iowa, Dec. 28, 1929. Contribution from the Entomological Laboratory of the Bussey Institution, Harvard Uuiversity, No. 331.

food by a very large percentage of the species. This is paralleled almost nowhere else in the animal or plant kingdoms, with the notable exception of certain parasitic organisms. In the case of these parasitic types, such as pathogenic bacteria, fungi and worms, it has of course never been questioned that they are important factors in influencing the abundance, distribution and, finally, the evolution of their hosts and of competing organisms. The same is self-evident with respect to parasitic insects, including those that carry diseases, and the recognition of the role played by entomophagous parasites has led to the development of the method of biological control that we have applied with success to the reduction of noxious insects. Such facts are so generally appreciated that we must not allow them to draw our attention at the present time from the less patent relationships that I wish to discuss.

The conventional classification of food habits as first applied to vertebrate animals, and later extended to other less familiar groups may be readily applied to insects and we may thus more or less accurately group them in the following categories which are by no means either clear-cut or mutually exclusive, since they may grade into one another or appear in combination in the diet of a single species of insect.

OMNIVOROUS = PANTOPHAGOUS
HERBIVOROUS = PHYTOPHAGOUS
PUTRIVOROUS = SAPROPHAGOUS
minimivorous = microphagous
fungivorous = mycetophagous
CARNIVOROUS = ZOOPHAGOUS
predatory = harpactophagous
parasitic = biophagous

So far as insects are concerned it is difficult to arrange these in any linear order and certainly no single arrangement could be made which would indicate the phylogenetic sequence of the different types in the several major groups where they occur. Every type except the parasitic one is to be found among the most generalized groups of insects. Thus, the omnivorous cockroach, the vegetarian walking stick, or the predatory dragonfly are to-day emulating their forebears who feasted likewise in the forests of carboniferous times.

It may seem idle to speculate concerning the most primitive type of food habits among the insects, although there seems good reason to believe that the earliest insects, like their somewhat problematical ancestors, may have subsisted upon dead or moribund animals in combination with miscellaneous plant material, or to speak more concisely, in terms of human dietetics, the balanced chop suey ration mentioned a few moments ago.

Such was undoubtedly the diet of the early multitudinous cockroaches that swarmed throughout those carboniferous forests. These very insects are today a prominent feature of the entomological fauna of tropical jungles, and, moreover, they have even invaded the overheated tenements of our great cities. The cockroaches, therefore, show three characteristic features: a mixed, more or less indiscriminate diet; great morphological stability over extended periods of time, and an adaptability to changing conditions and to intensive competition with other, more modern types of insects.

On the other hand, purely carnivorous habits are characteristic of several very primitive groups, notably of the earliest dragonflies. The predatory habits of these insects are very pronounced and predatism has attained a wonderful degree of perfection among the modern dragonflies. The imagines are admirably fitted for the capture of prey while on the wing, and the nymphs are even more marvelously adapted for the seizure of prey beneath the water in which they live. The mechanism peculiar to the nymph and unparalleled elsewhere is a unique, pincers-like, bristly organ, known as the mask formed by the highly modified labium. The form of this structure is so similar throughout the Odonata that there can be no doubt that it was characteristic of the earliest representatives of the order and perhaps of the ancestral Protodonata as well. So far then, as structural adaptation is concerned, the dragonflies must be rated very high. They have persisted over an extremely long period with little more tendency toward morphological change or speciation than the cockroaches. Even though the nymphal mouthparts are most exquisitely suited for the unfailing capture of prey, the diet of individual genera and species has not become highly specialized. We might

almost say that the great efficacy of the mask has made unnecessary any great specialization in instinct; and, consequently, the diet of any species or individual varies greatly, depending upon circumstances. This statement is abundantly supported by observations made on the diet of dragonfly nymphs by several entomologists. These show that there is practically no selection since the imagines of a single species of dragonfly will devour a greatly diverse mixture of insects, while the nymphs consume also many small crustaceans, other invertebrates, and even some Protozoa.

Among the dragonflies, then, a long history with comparatively slow evolutionary change is associated with an indiscriminate diet during both the nymphal and reproductive stages.

If we now turn to certain predatory types among some of the more recent holometabolous insects we find a condition strikingly in contrast to that just described. In the Diptera, for example, there is a series of rather closely related families, that includes the robber-flies or Asilidæ, whose members are highly predaceous. Although only fragmentary data are available for these flies, some species are seen to have very strong predilections in the choice of prey. Thus, among the large flies of the genus Proctacanthus, one species captures almost entirely aculeate Hymenoptera, more than half of its prey consisting of honeybees and hornets, while the second greatly prefers small scarabæid beetles in combination with other miscellaneous insects. Other robber-flies are butterfly hunters, but many are more or less general feeders, and a tabulation shows that, although there is a consistent choice of food among species, there is not the close restriction that prevails among parasitic insects, nor among vegetarian types which we will discuss in a moment.

A very high specificity in the selection of prey obtains among the solitary wasps. With these insects the prey is stung and stored in the nest, where it forms the food of the developing larva. Thus, the choice of food rests with the mother wasp, while the larva obediently eats what is put before it, thriving to maturity thereon. Although a very wide range of prey, including spiders and the most diverse insects is utilized by these wasps, individual species com-

monly restrict their hunting to the capture of a series of related forms or even to a single species. One American Aphilanthops stores only queen ants and a related European wasp captures ants also. Our common American mud-dauber wasps collect small spiders of various kinds and certain crabronids capture flies of a single or of several species. The fixity and persistence of their instincts is shown by the tendency of genera or larger groups to restrict themselves to related types of prey, and this may extend to the members of a large family like the Psammocharidæ, where the spider-storing habit is so general that the vernacular name of "spider wasps" has been bestowed upon them by common consent. In another group, stages through which the change from a somewhat indiscriminate diet to a specific one has taken place are still preserved. Thus, in the genus Sphex (Chlorion) some species store a variety of Orthoptera in their nests, others only a few, and finally some only one. As we shall see in a moment this condition prevailing among the solitary wasps is wholly analagous to that which obtains among phytophagous insects.

The tendency among these diverse types of predatory insects is clearly toward a restriction of the dietary although we cannot consistently detect any orderly arrangement whereby a relationship of predators implies to any great extent a similarity of prey. Sufficient evidence has been presented, however, to show that we cannot make any broad generalizations. Thus predaceous insects do not exhibit the close correlations characteristic of parasites nor of vegetarian insects. At this point, we must emphasize the fact that many predatory insects have narrowed down their food relations to a point where their direct contacts with the environment are restricted to certain definite components of the fauna of which they themselves form an integral part. The significance of these facts may be best understood after we have examined the food relations of vegetarian insects.

Insects that feed on plants are far and away the most important series to illustrate the adherence of species or larger groups to restrict diet. On account of their complex relationships toward these plants directly, and indirectly

through them to other animals, coupled with their great abundance and diversity, they are of extreme interest. Their ecological relations are far reaching for they extend, tentacle-like, into the innermost corners of every type of terrestrial, aerial, or fresh-water environment. From the general biological or evolutionary standpoint they are of peculiar interest for it is this vast horde of vegetarian species (for they include about half of the living kinds of insects) that have made their influence felt over the long lapse of geological time since these types became highly differentiated during the periods preceding the tertiary. The chronology of this process, at least with regard to specific food relations, is difficult to determine, but taxonomic groups similar to those of today were so well established in the eocene and oligocene that we can rest assured that their food relations were already equally complex at that time. Thus, the time during which the factors introduced by these insects have been active in affecting the evolution of other animals and plants is much more extended than that included in the period just mentioned. As I have shown previously, there is good reason to believe that the differentiation of feeding habits among phytophagous Coleoptera was well under way while that of the Lepidoptera was just beginning at the time when the modern types of trees appeared on the earth.

There is no need to attempt at the present time any detailed account of the specificity of food selection among the Lepidoptera as this is well known and I have already dealt extensively with it elsewhere. Briefly, we may say that the members of this order may be considered as forming two or three groups with respect to specificity of food. These are: first, those which utilize a very considerable and not necessarily related series of food plants, occasionally a hundred or more in number, like the cecropia moth or the leopard moth; second, those having a much more restricted dietary that includes a few, usually related, species; and finally, some that are confined to a single plant host or to several very closely related and genetically similar members of a single genus. Again, these categorical divisions are only relative; but experience shows them to be very convenient, and we may unquestionably regard them as successive phylogenetic stages. We may conveniently refer to

the insects concerned as polyphagous, oligophagous and monophagous, respectively.

The labors of economic entomologists have gone far toward an elucidation of the interactions of these several types of food-habits as they determine the competition for food among insects and the devious ways in which they influence the biocœnotic relations of insect food plants. And, since no plants appear to be immune to insect attack this question is seen at once to involve the whole terrestrial flora.

Several factors concerned in these relationships between insects and plants may be considered separately. The effect of insect feeding on the flora is by no means the same in the case of polyphagous, oligophagous and monophagous species. With the former a long series of plants suffer to a more or less equal degree. Thus, with grasshopper outbreaks there is general injury to all kinds of vegetation; with the gypsy moth a considerable series of trees and also other plants suffer, but not to an equal extent. This means that there is a simultaneous reduction in the abundance of a number of different plants, and an opportunity is offered for many others to increase, at least temporarily, while many competing insects decline due to a lessened food supply. Thus, in brief, outbreaks or fluctuations among polyphagous species involve many other insects and plants to a major extent. We can also see how such feeding might actually cause the extinction of certain rare or poorly adapted plants.

The feeding of oligophagous insects results in the injury to a greatly restricted series of plants and has, of course, no direct effect upon any others. If dominant species of plants be affected there as a very considerable opportunity for many rarer forms to increase, while if a reverse condition prevails and the scarcer forms are affected, the influence upon the remainder of the competing flora is negligible. Incidentally we must notice that the extinction of certain plants might result from the feeding of oligophagous species, although the chances for such an occurrence are less than those noted above in the case of polyphagous insects since a great reduction in one of a few food plants will at once considerably reduce the food supply. This is then immediately reflected in a lesser abundance of the in-

sect, and injury decreases. In general, therefore, the feeding of oligophagous insects does not involve simultaneous fluctuations in a considerable number of plants, especially if those concerned are not dominant forms, and likewise, a smaller number of species of insects is affected directly. The fluctuations that may occur among associated insects are to a greater extent in an inverse ratio rather than in a direct one.

Monophagous species present a very remarkable series of phenomena. Aside from any parasites they may support or predators that they may feed, their relations to the living environment are entirely restricted to contacts through the medium of the host plant. They can never become so abundant as to rise up and destroy it, since for obvious reasons their fluctuations in abundance trail very closely those of their host plants. Therefore, we may never attribute the extinction of any plant, even in a restricted region, exclusively to the activities of a monophagous insect. Other plants are affected to a varying extent, dependent mainly upon the rarity or abundance of the host plant. If it be a dominant species, its fluctuations increase or decrease the struggle for existence among competing plants; if it be a rare species, this influence upon a series of other plants is negligible. It also affects a number of associated insects which feed upon the same food plant. The number of these is, of course, extremely variable, but careful studies of plant faunæ indicate that dominant types of plants support surprisingly large numbers of vegetarian insects mounting into hundreds of species in the case of common types such as willows, figs, oaks and maize, although the average for plants in general falls far below this mark. Certain plants which produce poisons or violently irritating substances, (like our common American poison-ivy), enjoy comparative, but by no means complete immunity from injury by phytophagous insects.

In regard to their relations with the living environment, we may say that monophagous insects live a life apart. Their association with plants is such that the vicissitudes of life for both members of the pair are greatly reduced on account of the lesser number of variable factors that affect each. So far as abundance of fluctuation in numbers they

are mutually adaptive. The instincts determining food selection are firmly fixed in the germ-plasm and the insect is doomed to feed to the end of its days on beans, cabbage, yeast or what-not, unless some fortunate shift or mutation of instinct may add pork to the beans, or perchance combine hops and malt with the yeast ration. Such persistence over long periods during which whole groups of insects and plants have evolved in mutual adaptation seem only to be explained on the basis of instinctive behavior. This view which I have upheld in the past has been recently questioned by some, who would place the matter upon a purely physiological basis, but I cannot see that there is convincing evidence to support this conclusion or to controvert my own contentions that we are dealing with persistent instincts rather than with digestive necessities.

With the foregoing considerations on phytophagous insects as a basis it is possible to draw certain conclusions of a general nature which indicate some of the ways in which the development of oligophagy and monophagy has influenced the evolution of the higher plants as well as that of the insects themselves. Due to its tendency to reduce the chances of extinction of plant species whose existence might be jeopardized by an abundance of polyphagous insects we can see that it has tended to increase the diversity of the flora. The development of many mutual adaptations of plants with both monophagous and oligophagous insects are dependent upon the specific food habits of the insects concerned and it is thus clear that we must attribute to the development of these instincts many of the remarkable morphological modifications seen in both plants and insects. In the present state of our knowledge, at least, there is no other causal explanation for their existence. Since speciation and the rapidity of evolutionary change in general are highly correlated with adaptive modifications, we must attribute to the phenomena of restricted food a highly important role in determining the trend of these evolutionary processes.

A relationship similar to the one just given was early noticed by Darwin in connection with anthophilous insects and entomophilous flowers and his interpretation of the mutual modifications of insects and flowers has long since

become solidly entrenched among the unassailable biological doctrines, after having further engaged the attention of a score of later naturalists. I mention it here not for discussion, but only to show the similarity to to views just expressed concerning phytophagous insects and their food-plants.

Really no time remains for the discussion of the other types of food habits among insects which I had hoped to mention in connection with their biological interest. They would serve to clarify the statements already made, but since they might also cloud the issue somewhat and since they show how thoroughly the insects have exploited the world's food supply they are more appropriately dealt with in connection with my concluding remarks on insect food as viewed from the human standpoint.

From a purely human standpoint, we must regard everything as either beneficial or harmful, unless it appear to be utterly unimportant or indifferent and the scientific mind will not admit the third possiblity. As entomologists are prone to look upon insects in this light we may view them thus at the moment.

INJURIOUS INSECTS

harmful to man directly
harmful to useful plants
harmful to useful animals
a. harmful to useful insects

BENEFICIAL INSECTS

destroyers of injurious insects
destroyers of undesirable plants
destroyers of obnoxious substances
producers of useful substances.

I think this classification reflects the usual attitude toward the economic relations of insects, and it serves well to emphasize the fact that the importance of every species is gauged by what it harms, injures or destroys, with the sole exception of the small handful of "producers" like the

honey bee, silkworm, etc. This can only mean that, practically, the activities of insects that appear to be of greatest human interest, are those which serve to destroy other things. As the ultimate purpose of the human species is to destroy and make over the face of nature, quite naturally insects and man are at once both in accord and conflict, and our most competent practical entomologists predict a battle to the death between insects and man. Unfortunately for ourselves, man has proceeded to change the face of nature as rapidly and completely as possible. In so doing, he has found his progress seriously impeded by an unforseen increase in the numbers of insects that feed upon agricultural, horticultural and forest crops, combined with an equally unexpected migration or spread of many phytophagous species into regions where they did not previously occur. There is no need to press this point for we all realize that this is a serious situation that confronts agriculture, horticulture and forestry today. It is equally clear that this distressing condition has been brought about mainly by two factors inherent in our prevailing mode and philosophy of life. One is the growing tendency throughout the world, and particularly in America, to devote more and more extensive areas to the propagation of easily managed crops that give promise of large pecuniary returns. This matter then goes deep into the fabric of our commercial life. The other factor concerned is the unprecedented increase in the bulk and variety of vegetables, fruits and food-stuffs of all kinds that are shipped here and there in all directions, aften to the uttermost corners of the earth wherever they may be disposed of at a profit. If, as generally occurs, there is great local over-production of certain foods, the urge for wider distributional opportunities is so powerful that it must needs invoke the aid of advertising propaganda and every other known method that may be put to the tune of modern jazz. No one has ever suggested the curtailment of such shipping on economic grounds. This matter is, of course, likewise not a suitable subject for unbiased discussion except in purely academic circles, since it is too deeply concerned with the business of transportation, with advertising, with the love of luxury and with other matters of vast and immediate pecuniary importance.

Having thus bared a very pessimistic attitude and exposed to view what you have doubtless recognized as the clear, clinical picture of an inferiority complex, let us return to some purely entomological phases of the matter. How do the several types of food-habits among vegetarian insects affect their pracitical importance in relation to the human food supply? It is generally conceded that monophagous and oligophagous types are the ones most destructive to cultivated crops. We can at once recall a long series of such species, the potato-beetle, the codling moth, the oriental peach moth, and many others whose importance is due to the fact that they unerringly pick out valuable and widely cultivated agricultural plants. On the other hand, many with a considerable range of food-plants, the bollworm, the corn-borer, the Mediterranean fruit fly, the melon aphid, the red scale and the like are very destructive, but quite generally less so on the whole, in spite of the much greater variety which may feed upon a particular species of plant. General feeders like the various types of locusts, army worms, etc., although very conspicuously destructive in some regions and on certain occasions, are in the long run less generally dreaded by agriculturists. To return then to our earlier discussion of monophagy and oligophagy, we must admit, without further ado, that our present civilization could well dispense with this interesting evolutionary phenomenon, since it is a gift of Nature that serves to increase injury to cultivated plants, at least under modern agricultural conditions. We might return the gift with thanks, but so far, science has been unable to write a sufficiently polite or forceful note to accompany the transfer.

There is just one more matter relating to these destructive insects which I hesitate to mention as it is so familiar to all of us. It was one of the first choice bits of information we acquired as students and we have religiously passed it on to our students ever since. The most destructive insect pests are those that have spread from their original habitat into some other faunal region. The reasons for this are usually said to be well understood on the basis of predatory and parasitic control, but there is much to suggest that other factors remain still to be elucidated.

Since human behavior is conventionally regulated by prohibitions, punishments and legislative action of endless variety, it is quite natural that the immigration of insects should have come to the attention of law-makers as a fit subject for similarly paternal consideration. The protection of the human population from communicable diseases by restricting the movements of diseased persons has been so satisfactorily effected by quarantine measures that excludatory regulations have been instituted to protect countries from invasion by insects from other regions, without a clear statement that the two situations are neither identical nor essentially similar. Thus, such regulations have been based upon the inspection of host plants or other materials. The success of these has not been all that might have been hoped and there is a wide divergence of opinion as to whether the results attained are in any sense commensurate with the great expense and hardships entailed. It is quite clear that the absolute exclusion of insects is a much more difficult undertaking than the interception of cases of human disease. Human beings are dealt with legally and otherwise as individuals and besides, the success of public health measures does not depend upon absolute exclusion for all time. There is no question that such measures must aid somewhat to delay the introduction of insect pests where some natural geographical barrier to animal or plant migration exists. As time goes on, as transportation increases and speeds up and as movement becomes our main interest, the poor old oceans, mountains and deserts are rapidly losing their importance as separating faunas and floras. In our own country during the past few years there has also been an increasing movement to prevent the spread of particular species of insects between states or other artificially limited areas where absolutely no natural barriers exist. This in itself is a most commendable endeavor when it can be carried on unostentatiously and at reasonable expenditure, since it serves to delay the otherwise extremely rapid naturalization of insects over contiguous areas. In some instances it is obvious that such quarantines may become oppressive and entail expenditures and economic consequences to communities that are not at all warranted by any advantages that might reasonably be expected to accrue

from them. This is well illustrated by the supreme efforts made to curb the spread of the Mediterranean fruit fly following the recent discovery of its establishment in Florida. Many persons were even led to believe that the extermination of this pest in the United States was a foregone conclusion instead of a hoped-for miracle. Certainly long experience in connection with the establishment of exotic insect pests of cultivated plants holds out little prospect of their eradication. Another unfortunate circumstance in this connection is the great menace of repeated introductions of the same insect. I do not wish to pose as a critic of the legislative activities of entomologists but feel that it is our duty to view such matters in an unbiased attitude and to shy clear of the idea that all evils may be remedied by the enactment of laws and the expenditure of money. The use of the quarantine has increased at such a rapid rate that we should be sure of our ground before allowing it to usurp the foreground of entomological practice. Another grave danger lies in the fact that perfectly sane scientific pronouncements may be easily perverted by legislative enactment and subsequent enforcement by persons far less expert than the entomological authorities who formulated them.

Certainly the importance of these problems and the threat which they hold over our future comfort and welfare demand that we as entomologists approach them in an altruistic spirit.

A REVIEW OF OUR PRESENT KNOWLEDGE OF THE GEOLOGICAL HISTORY OF THE INSECTS.[1]

By F. M. Carpenter.

During the past ten years, subsequent to the publication of Handlirsch's general account of fossil insects in Schröder's "Handbuch der Entomologie" in 1920, many important and unexpected specimens have been discovered. So profound an effect have these new fossils had upon insect paleontology that I venture to invite your attention this evening to a review of our present knowledge of the geological history of the insects, and to a discussion of the main problems which await solution.

First, let us consider what important discoveries the past decade has witnessed.[2] The Carboniferous rocks, unfortunately, have not made a very large or an unusual contribution. The British coal measure insects, comprising sixty species, have been monographed by Bolton in a work which has added a great deal to our knowledge of certain extinct orders. Pruvost has described a splendid series of new fossils collected at the famous Commentry beds in the central plateau of France, and Bolton has published on a smaller assemblage of insects from the same locality and now contained in the British Museum. In this country, Cockerell has written a comprehensive account of the Carboniferous insects of Maryland. But interesting as all these coal measure insects are, they seem to be quite typical of those which have previously been found in this horizon,

[1]Annual address of the retiring president of the Cambridge Entomological Club, Jan. 14, 1930. Contribution from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 330.

[2]Although Handlirsch's account of fossil insects in the "Handbuch" was published in 1920, it did not include the results of several important works which appeared a few years earlier. For this reason, the latter (as Tillyard's "Mesozoic Insects of Queensland") are mentioned here.

including such groups as the Paleodictyoptera, the Blattaria, the Megasecoptera, etc. In marked contrast to this, the Permian has unexpectedly furnished us with a remarkable series of specimens, representing groups which have not previously been reported from this horizon. In 1920 Handlirsch listed from the Permian 97 species of insects, aside from cockroaches; now there over 250, also exclusive of cockroaches, and many additional species are contained in unworked collections recently obtained from Permian deposits. For the most part, these new fossils have been secured at three widely separated localities, in Australia, North Russia, and Kansas. The Australian and Kansan specimens have almost exclusively been studied by Tillyard, while the Russian material has been investigated by Martynov. Of course such fossils have thrown much light on the geological ranges and the phylogenetic origin of our existing groups of insects. We now know that many recent orders had a much longer geological history than had been supposed; for the first time the Mecoptera, Neuroptera, Coleoptera, Diptera, Odonata, Homoptera, Psocoptera, and Orthoptera[3] have been found in the Paleozoic.

The Mesozoic has likewise contributed much to our collections during the past decade. The Triassic, which had previously been nearly a blank as far as insects were concerned, is now represented by about 120 species, described by Tillyard from Queensland. Martynov has published on another remarkable series from the Jurassic of Turkestan, and his studies are by no means complete. Mention should also be made of Tillyard's monograph of the Liassic dragonflies of England, and Ping's study of the Cretaceous insects of China. The latter work is particularly interesting since it has brought to light the only promising insect deposit of the Cretaceous which has yet been found.

The Tertiary, of course, has played a large part in the recent advances of insect paleontology. The Baltic amber insects have received much attention at the hands of several specialists; certain groups, as the Thysanura, Colembola, and Paussidae, have been completely revised. Cockerell has continued his description of the Florissant and Green River

[3]Undescribed.

insects, as well as those of the Tertiary of England and others contained in the Burmese amber. Very recently Martynov has described the insect fauna of a newly discovered Tertiary bed in Russia, and Pongraz has written several papers on the fossil insects of Hungary, redescribing many obscure insects which Heer first studied seventy years ago. A few Tertiary insects have been collected at new localities in this hemisphere,—in Tennessee, Washington, Nevada, and Argentina, all of which give much promise of providing us with a more complete series of fossils in the future.

If we take the conventional bird's-eye view of the geological history of the insects, we are at once struck by the antiquity, not only of their natural groups, such as the orders, families, and genera, but of their habits and ethology. As far back as the Oligocene, about 50 million years ago, the social Hymenoptera had already differentiated into several castes, and the ants, at least, had accomplished this by the Middle Eocene. The Baltic amber ants, as demonstrated by Wheeler, show definite polymorphism and even the higher stages of development such as ergatoid and pseudogynic females, and ergatomorphic males. Some of these Oligocene ants had also "learned to attend" plant-lice, just as many of the modern species do. Whether or not some of the amber insects belong to species which are still existing on earth, is an open question. In the case of the ants, there are eight species which are morphologically identical with certain living ones. If these species actually are identical —and there is no evidence to the contrary—then they have existed without apparent structural change for some 50 million years[4]. Aside from the probability of the specific identity of some of our fossil and recent insects, it is certain that most of the genera of the Tertiary are still surviving. Of course many of the genera which used to be more or less cosmopolitan, these many millions of years ago, are now restricted to much smaller areas,—as the dipterous genus, *Glossina* or the formicid, *Oecophylla*. As we become more and more acquainted with the tropical insect

[4]I have used the time estimates advanced by Dr. A. Holmes, in his "Age of the Earth" (London, 1927).

faunas, we even find genera which were first known to us only as fossils and supposed to have been extinct. Such a genus is *Archipsocus*, described by Hagen for an amber Psocid, but subsequently found to be existing in the tropics of both the New and the Old World. Another instance is the ant *Gesomyrmex*, which was originally described by Mayr from the amber, and which was found many years later in the region of Borneo.

Now if we go back another hundred million years on the geological calendar, to the Middle Mesozoic, we are unable to recognize definitely any existing genera, but we do find many families quite familiar to us at the present time. Of course, as one would naturally expect, there is a marked difference in the development of the several orders. All the Mesozoic Trichoptera, for example, belong to extinct families, but many of the Orthoptera and Diptera can be included within modern families. When we reach the Permian, another 50 million years away, we observe that our recent families no longer make their appearance, but we are still able to recognize several existing orders, as the Mecoptera, Neuroptera, Odonata, Diptera, etc., including types with complete metamorphosis. However, receding another 50 million years—making a total of about 250 million—we come to the Upper Carboniferous, in which our earliest winged insects have been found. Here we find an assemblage quite unlike that of any other period, including such primitive forms as the Paleodictyoptera, and a few more highly specialized groups as the Protodonata and Megasecoptera. Only one recent order, Blattaria, has been recognized without question in the Upper Carboniferous[5]. Tillyard has described from even older rocks, the Devonian of Scotland, the remains of some arthropods which he considers to be true Collembola, but I do not believe that entomologists in general have accepted his conclusions. The absence of winged insects from strata below the Upper Carboniferous is particularly disconcerting, for, primitive as these coal measure insects may be, they are nevertheless

[5]Tillyard maintains that the obscure *Metropator pusilus* Handl., from the Pottsville series of the Upper Carboniferous, is a true Mecopteran, but this is very dubious. See G. C. Crampton's discussion, Psyche, 37, 1930; p. 93.

perfectly respectable insects and so far along the line of the Insecta that they show no definite relationship with other Arthropods.

With this general survey of insect paleontology in mind, I suggest that we now examine more carefully the geological ranges of the larger and more prominent insect orders. Of the extinct ones certainly the most interesting, phylogenetically, is the Paleodictyoptera. These generalized creatures, which are usually regarded as the ancestors of all the other winged groups, were developed into many diversified families before the end of the Carboniferous; but for some reason their glory was brought to an abrupt end, for only one species is known to have persisted into the Permian. Another interesting Carboniferous order was the Megasecoptera, the members of which were unique among the other known species of the period in that they possessed petiolate wings, not very much unlike those of the damselflies. These insects appear to have completely died out before the Permian, but some recent groups are supposed to be their direct descendants,—as the Odonata and Mecoptera. The order Protodonata, another assemblage which has never been found living, is especially famous because of the large size attained by some of its members, *Meganeura* of the Commentry of France having a wing-expanse of about 29 inches. This order, in contrast to the foregoing, persisted through the Permian, but apparently became extinct during the Triassic. All the rest of the Carboniferous insects, excluding a few very small orders with obscure affinities, seem to fall into what we may call the Blattoid, or cockroach, complex. Handlirsch and others have attempted to divide them into separate orders, such as the Protorthoptera and Protoblattaria, but these groups overlap in many respects. This complex, in my opinion, represents the converging branches which later lead to several distinct orders of insects; it represents, in other words, the trunk of the conventional phylogenetic tree, where the several branches had joined—or were in the act of joining—into one. I suspect that as more and more Upper Carboniferous insects are found this complex will become even more jumbled; and I also believe that when Lower Carboniferous insects are discovered, as they eventually must, we shall find the Paleo-

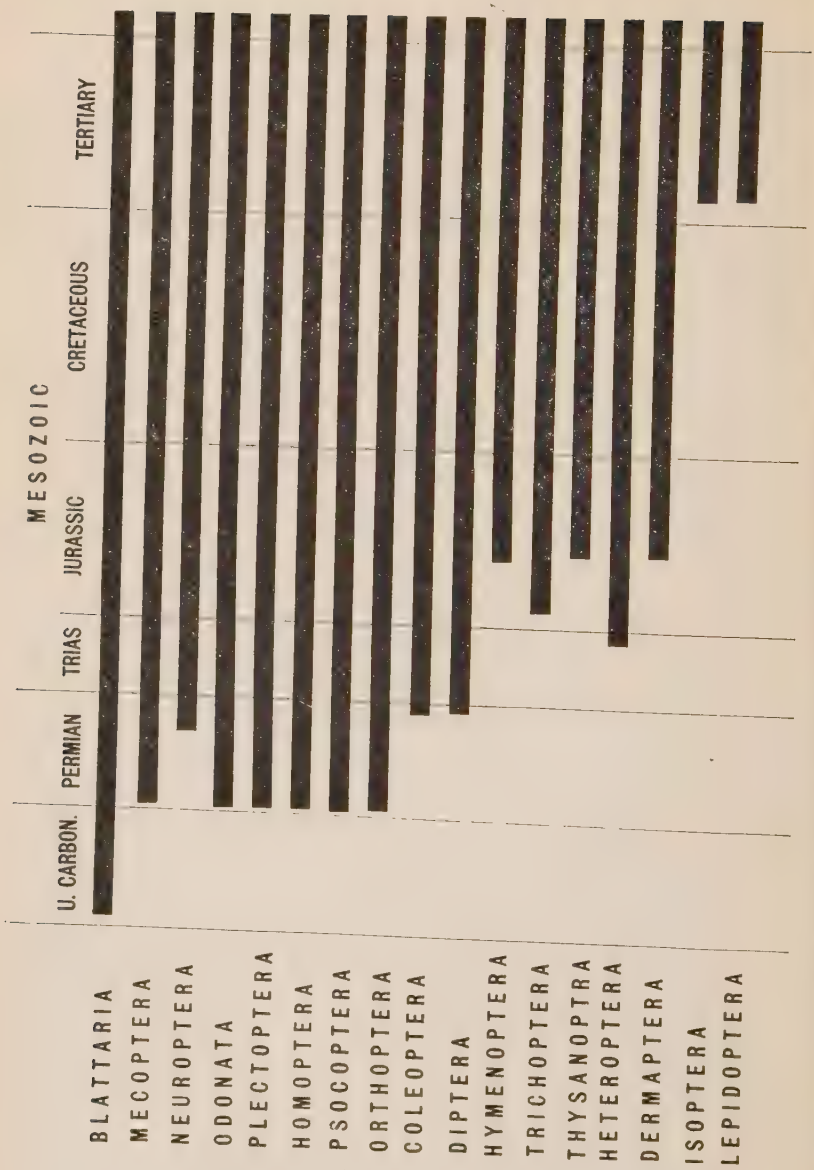

PLATE 1.

Table 1. Geological Ranges of the Larger Insect Orders.

dictyoptera, Megasecoptera, and the other extinct orders of the Upper Carboniferous, joining with this complex.

If we examine a diagram showing the geological ranges of the larger existing orders of insects, we are at once impressed by the fact that ten of them have been found in the Permian; of these, seven have been recognized in the Lower Permian, and one, the Blattids, in the Upper Carboniferous. These ten Permian orders are a rather diversified lot, including the Mecoptera, Neuroptera, Odonata, Homoptera, Psocoptera, Coleoptera, Diptera, Plectoptera, Blattaria, and Orthoptera. Since their occurrence in the Permian marks the earliest record of all these insects, except the cockroaches, let us see if these ancient representatives are as primitive as we might expect.

The presence of Mecoptera in the Lower Permian is particularly striking, inasmuch as our recent members of this order develop with complete metamorphosis. Of course since no larval or pupal forms of the Permian Mecoptera have been found, we have no direct evidence that they, too, were holometabolous; but, as Tillyard has pointed out, they are so close to our existing types in other respects that no one would deny that they also possessed holometabolism. There are many features of these ancient scorpion-flies that are most unusual. Those from the Lower Permian of Kansas, with which we are best acquainted, are very minute, having an expanse of about 10 mm.,—less than that of any existing species. Some of the Permian forms had short beaks, like those of the Australian Choristidae; the antennae were shortened and possessed fewer segments than those of any known Mecopteran except the highly specialized Bittacidae; the males of some genera had a genital structure essentially like that of the Bittacidae, also. Finally, some of the Lower Permian species had a wing venation more highly specialized than that of any recent types. The Neuroptera have not yet been taken in the Lower Permian, but those of the Upper Permian were actually more specialized in their venation than their existing relatives. Both the Planipennia and Megaloptera were already differentiated and as highly developed along their own lines as the Mecoptera were along theirs. Although Tillyard maintains that the absence of Neuroptera in the Lower Permian collections is sufficient to show that the

order was a later development than the Mecoptera, I believe that the Upper Permian specimens demonstrate that the Neuroptera are at least as old a group as the Mecoptera. The finding of true Odonata in the Lower Permian was one of the surprising discoveries of the decade; previously no Odonata had been known from the Paleozoic, but subsequent to the finding of the Lower Permian fossils, an Upper Permian species has also been located. All these described Permian forms possessed petiolate wings, more narrow and elongate than any recent types. As in the case of the Mecoptera, the Permian Odonata were very small, some having a wing-expanse of about 4.0 cm. The absence of Odonata with broad wings basally from the Permian has lead Tillyard to the conclusion that the Anisoptera and the Anisozygoptera were derived from the petiolate Zygoptera during the Triassic. For my own part, I do not accept this inference, but consider that both the anisopterous and zygopterous lines were already developed during the close of the Upper Carboniferous. The occurrence of true Homoptera in the Lower Permian is of much significance, especially since we are forced to admit that they appear to be the most highly specialized of all the insects of this horizon. Numerous Homoptera, even more highly developed, have been taken in the Upper Permian of Australia and Russia. The finding of Psocids in the Lower Permian was perhaps the most surprising discovery made in the field of fossil insects for many years. At the time when these fossils were collected, the earliest record of the order was in the Baltic amber, of Tertiary age, some 200 million years later, but subsequent to the finding of the Permian specimens, Martynov has taken others in the Jurassic of Turkestan. The Permian Psocids were very similar in venation to the Homoptera, and were nearly as highly specialized. The Plectoptera or Ephemerida have long been recognized as very primitive insects, so their presence in Lower Permian beds is not at all surprising. The Permian species, although more primitive than any recent forms, were nevertheless well developed along certain lines and show that the order originated far in the past. The other Permian orders, the Diptera, Orthoptera, and Coleoptera, are too sparsely represented in our collections just now to enable us to form any definite idea as to how far they had developed along their

particular lines of evolution. But I believe that it is already evident from our discussion of the preceding groups that the Permian orders were far more highly specialized than they should be in the strata where they first make their appearance. Some of them, in fact, such as the Mecoptera, Neuroptera, Odonata, Homoptera, and Psocoptera, were so highly developed that they must have extended as distinct orders well back into the Carboniferous. Now if this is the case, one might wonder why these insects have not been found in the Upper Carboniferous. The explanation, I believe, lies in the coarse nature of the Carboniferous strata in which the insects are preserved. The Lower Permian representatives of the Mecoptera, Odonata, Homoptera, and Psocoptera are very small, those of the first two orders being much smaller than the average existing species of these groups; and all the Neuroptera of the Russian Permian and most of those of the Australian Permian (which is almost Triassic) are also small, their averaging wing-expanse being about two centimeters. The majority of the Carboniferous insect beds are composed of coarse material, and even the finest of them would hardly be capable of preserving such minute insects as those which we have just considered from the Permian. The average wing-expanse of the Carboniferous insects was approximately 10 cm., not including the cockroaches. The wings of the latter were much smaller, but they also possessed the coriaceous texture of the recent species, and were consequently able to be preserved regardless of their smaller dimensions. This selective nature of the Carboniferous strata has given rise to the notion that all the Carboniferous insects were "giants"; but I do not believe this to be the fact, and predict that when some enterprising geologist discovers for us a Carboniferous insect bed with as perfect a preservation as the Wellington shales of Kansas, we shall find some very small insects belonging to the several recent orders which are so highly developed in the Permian.

Let us now consider the orders of insects which make their first appearance in the Mesozoic. There are five of these: the Trichoptera, Heteroptera, Dermaptera, Hymenoptera, and Thysanoptera. Only one, the Heteroptera, has been found in the Triassic; the others are not known earlier than the Jurassic. These oldest Heteroptera were so well

developed along the lines of the recent species that it seems almost certain that the order must have existed in the Permian. The Trichoptera of the Jurassic, on the other hand, are essentially more primitive than the extant species, many of them possessing a venation so similar to that of their contemporary Mecoptera that it is frequently difficult to distinguish the members of these two orders. Consequently, it is very doubtful if the caddis-flies will ever be found lower than the Triassic. The Hymenoptera are first represented in the Jurassic, by such forms as Siricoids, Oryssoids, and Ichneumonoids. This diversity of the Jurassic Hymenoptera makes it rather obvious that the order had been some time in existence before that period, probably at least as far back at the lower Triassic. The only known Mesozoic Dermaptera and Thysanoptera have been taken in the Turkestan beds, but they are both represented by characteristic types, not very much unlike certain recent species.

We are now left with the two orders whose first record is in the Tertiary rocks,—the Lepidoptera and Isoptera. Only very few Lepidoptera have been found as fossils in this horizon, but these are absolutely modern in every respect, and there can be no doubt that the group arose some time in the Mesozoic. The Isoptera are quite common in the Tertiary beds and are differentiated into many recent families, most of which, however, are now limited to much smaller geographical areas. There is every indication that the termites will some day turn up in Jurassic and perhaps even Triassic strata.

From the foregoing discussion of the geological ranges of the larger insect orders, it is obvious that by far most of the orders have had a longer history than one would assume from the mere geological occurrence of the oldest species. In every case where we have enough fossils to utilize, we see that the earliest representatives of each order are relatively highly specialized along the lines of the recent types; and this is particularly true of the Permian record. In order to have our diagram represent the probable true range of these orders, we must make several changes: The Mecoptera, Neuroptera, Odonata, Homoptera, Psocoptera, Plectoptera, and of course the Blattids, would extend back to the Upper Carboniferous; the Hemiptera would recede to the Permian, and the Trichoptera, Dermaptera, and

Thysanoptera to the Triassic, while the Lepidoptera and Isoptera would be shown as far back as the Jurassic only. Whether these estimations are substantiated or not will of course depend entirely upon the future discoveries in insect paleontology.

There is one other aspect of insect paleontology which I wish to discuss: the relative development of each order in the several geological periods. Those of you who have never considered this aspect of entomology will probably be more or less surprised at some of the facts. The average entomologist, if there be such a freak, is so accustomed to thinking of the insect orders in their present relative standings that he never stops to reflect that there must have been some period in the earth's history when the more predominant of the recent orders were actually struggling for a footing; when some of our smaller groups, now nearly extinct, were the predominant ones. Or perhaps the entomologist is, let us say, a hymenopterist, and so fond of his pets that he cannot imagine any period in the earth's history when they were not disconcertingly abundant. But a moment's reflection on the geological history of the other groups of animals will show that such a change in the relative status of the orders is only to be expected. Taking the fishes for an example, we note that the Lung Fishes, which are now represented by a very few species, were one of the most predominant groups during the Devonian and Carboniferous; in a similar manner the Lobe Fishes and the sharks were very abundant during the latter half of the Paleozoic, although both of these types are now greatly outnumbered by more recently evolved forms. Innumerable examples may also be found in the higher vertebrate classes. Among the Reptilia, the Order Crocodilia was represented in the middle Mesozoic by a great number of species, which are now reduced to a small fraction. An even more striking illustration is furnished by the Rhyncocephalia, which were well developed in the number of species during the Triassic, but are now known from a single living species, *Sphenodon punctata*, of New Zealand. It is only logical, therefore, that we should find that our insect orders have passed thru similar modifications.

I take it that no one will deny that the number of species in an order is an index to the "health" of that group. At least it is obvious that such an aggregation as the Coleoptera, with close to 200,000 existing species, is in less danger of becoming extinct within the next thousand years than, say, the Mecoptera, of which less than 200 species have been found in all regions of the earth. Consequently, an accurate idea of the "species strength" of the orders can be obtained by determining the percentage of species which each order contributes to the entire insect fauna. The present percentages for some of the existing orders are shown in the right-hand column of figure 2. Here we see that the Mecoptera, Neuroptera, Odonata, Psocoptera, Plectoptera, and Blattaria each make up less than 1% of the known species. The Orthoptera and Homoptera are but little better, with about 3% and 3.5% respectively. The Coleoptera lead with the striking figure of 41%.

TABLE NO. 2.

RELATIVE ABUNDANCE OF SPECIES IN EACH ORDER AT DIFFERENT PERIODS

(Figures in Percentages)

	Permian	Mesozoic	Tertiary	Recent
Mecoptera	9.0	3.7	.16	.035
Neuroptera	3.0	4.8	.50	.42
Odonata	.80	6.6	1.6	.56
Homoptera	12.5	9.0	4.0	3.4
Psocoptera	6.0	.25	.45	.12
Coleoptera	1.0	37.0	37.0	41.5
Plectoptera	3.5	2.0	.30	.095
Diptera	.30	5.0	27.0	10.8
Orthoptera	.30	9.0	1.2	2.9
Blattaria	34.0	7.0	.90	.42

Even a casual examination of the geological history of the insects will indicate that quite different conditions have prevailed. In the case of the Mecoptera, for instance: 10 species of these insects have been secured in the Lower Permian of Kansas, 4 species in the Russian Permian, and 15 in the Australian Permian, making a total of 29 species from these three deposits. Yet in the Tertiary, which has produced more than twenty times as many species of fossil insects as the Permian, we have found only a total of 12

Mecoptera in all deposits! When we put this on a percentage basis, the results are even more striking (table 2). We find that the Mecoptera make up about 9% of the Permian insect fauna, less than 4% of the Mesozoic, and not even .2% of the Tertiary; and as I have mentioned above, the Mecoptera contribute less than .04% to the recent species. The Neuroptera comprise about 3% of the Permian insects, nearly 5% of the Mesozoic, but less than 1% of the Tertiary and Recent. The Odonata are only represented in the Permian by less than 1%; but in the Mesozoic we find that almost 7% of the species belong here, while in the Tertiary the figures drop below 2%, and at the present time the Odonata make up about one-half of one per cent. The Homoptera, as I have stated above, are very common in the Permian beds, making up a total of about 12.5; in the Mesozoic this changes to 9%, in the Tertiary and Recent to a little less than 4%. The Psocoptera are also common in the Permian, making up 6% of the fauna; but less than .3% of the Mesozoic, .4% of the Tertiary and about .1% of the Recent. The Coleoptera are rare in the Permian, only about 1% of the species of this horizon belonging here; but in the Mesozoic, Tertiary and Recent about 40% of the species fall within this order. The Plectoptera make about 4% of the Permian insects, but this figure drops off gradually from the Mesozoic reaching about .1% at present. Approximately .3% of the Permian insects are Diptera, and this increases to 5% in the Mesozoic and 27% in the Tertiary, only to drop again in recent times to about 10%. The Orthoptera are as scarce in the Permian as the Diptera but increase to 9% in the Mesozoic, then fall off to about 2%. The Blattaria furnish us with an astonishing decline: in the Upper Carboniferous they composed about 57% of the entire insect world, as we know it; in the Permian, this figure became 34%; in the Mesozoic, 7%; and in the Tertiary and Recent, less than 1%.

I have presented these figures without any implications as to their significance, or without trying to interpret them. It is an undisputable fact that the Mecoptera include 9% of the known species of Permian insects, 4% of the Mesozoic, and .2% of the Tertiary. We now have to determine whether this variation is due merely to chance or to actual

variation in the specific standing of the groups during the several geological periods. Have the Mecoptera, for example, really been on the wane since the Lower Permian, or are the figures which indicate this without significance? To answer this question one might consider the correlation between the occurrence of the orders in the deposits of each horizon; if the percentages of each order even approximately agreed, we should have positive evidence of the value of our percentages. But this would be a long and tedious recital, so we must find another way of accomplishing similar results. Fortunately Handlirsch in 1908 included in his volume on fossil insects a list of the percentages of the orders, similar to the one which we have considered above. At that time there were 7651 species of fossil insects described. In 1920 Handlirsch again listed the percentages in a similar way for the fossils known at that time, a total of 9302 species. Now there are approximately 10,400 species of fossil insects recognized. That is to say, between the years 1908 and 1920, 1651 species of insects were described; and between 1920 and 1930, a total of 1100 more. These additional species represent the fossils that have been taken in new deposits, as well as those contained in new collections from previously known beds. A comparison, therefore, between the percentages obtained in 1908, 1910, and 1930, furnishes us with a means of determining how closely fossils in new localities, new deposits, and additional collections agree with older records, and consequently a means of determining whether or not our figures have any significance. In table 3 these percentages are listed in parallel columns. We observe at once, of course, the blankness of the Permian record before the 1930 column. This, as I have explained above, is due to the fact that practically no Permian collections had been worked before 1920. We have since found three widely separated Permian beds, each with a diversified fauna, and each sufficiently fossiliferous so that our total of Permian specimens is well over 7000. We cannot therefore check these Permian figures with earlier ones, to any extent. In 1908 Handlirsch placed the Permian blattids at about 80%. This was because Sellards had described only the cockroaches of the Kansan Permian at that time; in the 1920 column this

percentage dropped to 57%, for Sellards had by then described the Plectoptera, and a few other groups. Now that all the Permian orders have been studied, we find the figure at 34%, which is probably very close to the correct magnitude. Although we have no previous records to check with those of the 1930 columns, it is interesting that the insect faunas of the several Permian beds compare very closely, although neither the Kansan nor Australian Permian beds have been entirely worked out. We are therefore obliged to regard the Permian record as more or less temporary and probably subject to slight changes when additional material has been found. Just how great these changes are we cannot say at present.

TABLE 3.

RELATIVE ABUNDANCE OF SPECIES IN EACH ORDER AT DIFFERENT PERIODS, AS DETERMINED IN 1908, 1920, 1930

(Figures in Percentages)

	—Permian—			—Mesozoic—			—Tertiary—		
	1908	1920	1930	1908	1920	1930	1908	1920	1930
Mecoptera			9.0	2.0	3.3	3.7	.11	.13	.16
Neuroptera			3.0	4.0	4.1	4.8	.60	.62	.50
Odonata			.80	6.8	6.2	6.6	1.5	1.3	1.6
Homoptera			12.5	4.0	8.0	9.0	4.0	3.6	4.0
Pscoptera			6.0	.15	.15	.25	.40	.40	.45
Coleoptera			1.0	35.0	30.0	37.0	40.0	37.0	37.0
Plectoptera ...	2.8	7.5	3.5	1.8	1.8	2.0	.30	.20	.30
Diptera			.30	3.5	5.0	5.0	26.0	25.0	27.0
Orthoptera			.30	8.0	10.0	9.0	1.2	1.2	1.2
Blattaria	80.0	57.0	34.0	8.0	7.0	7.0	.70	1.0	.90

Leaving the Paleozoic and passing to the later formations, we note that at the present reckoning the Mecoptera make up about 3.7% of the Mesozoic insects. Although this is nearly twice the percentage obtained from the 1908 records, it is still vastly lower than the 9% of the Permian, and equally greater than the Tertiary percentage, which is quite constant in all of the columns. It seems very probable therefore that while the relative number of species of fossil Mecoptera may vary somewhat as additional beds are discovered, these variations will not be sufficient to upset the present trend in the figures, and we are quite safe—

as safe as any paleontologists—in concluding that the Mecoptera had reached their maximum during the Permian. The Neuroptera show a much more consistent series of figures during the Mesozoic and Tertiary, and it is doubtful in my mind that these percentages will change radically in the future. In this case, however, we see that the Neuroptera appear to make up a higher percentage of the Mesozoic fauna than the Permian one; but the difference is very slight, only a little over 1%, and since the Permian Neuroptera are quite as highly specialized as the Mecoptera of that period, it is very probable that a much larger number of Neuroptera will turn up in new beds. The Odonata in both Mesozoic and Tertiary have been regular in their occurrence, so that there has been hardly any variation in their percentages during the past twenty years. Here the maximum seems to be in the Mesozoic, and the difference between the Permian on the one hand, and the Tertiary on the other is so great (even more so than in the Mecoptera) that it is extremely doubtful that this trend will ever be disturbed. The next order, the Psocoptera, has apparently had a history similar to that of the Mecoptera. While the percentages of these insects in the Mesozoic and Tertiary have varied somewhat, due to the early neglect of these small insects, they are so abundant in the Permian that there are no grounds for supposing that they will ever turn up in the Mesozoic and Tertiary to a similar extent. The Homoptera are the same. It should be noted that there was a great increase in the percentage of the Mesozoic Homoptera between 1908 and 1920, again, as in the case of the Psocids, because these minute insects were not observed in the deposits until after the publication of Handlirsch's "Fossilen Insekten". At the present time, although the percentage of Mesozoic Homoptera is about 9% of the whole insect fauna of the period, it is very doubtful if this will ever increase to overtake the Permian ratio, where it is 12.5%. When we come to the Coleoptera, we see that the percentage of these in the Mesozoic and Tertiary has been quite stable in collections obtained during the past 20 years. The striking fact, of course, is the evenness of their relative abundance as fossil from the Mesozoic to the present, especially in contrast to the small percentage known in the

Permian. It is obvious, I think, that the jump from 1% in the Permian to 37% in the Mesozoic, is so great as to arouse one's suspicions as to the accuracy of the geological records of these insects. For my own part, I suspect that the fault lies with the Permian, not with the Mesozoic, and that a relatively larger number will be found in the Permian than we know at present; but it seems unlikely that the Permian ratio will ever approach that of the Mesozoic. The Diptera have likewise been constant in their occurrence in insect beds. It certainly does not seem logical that the Tertiary proportions, somewhere around 25% will ever be exceeded by those of the Mesozoic, which have not gone over 5%. Whether the Diptera were actually twice as abundant relatively in the Tertiary as they are at present, as our figures would indicate, is perhaps open to more question; there is certainly no reason why this order should not have attained its maximum during the Tertiary. When we pass to the Plectoptera or Ephemerids, we again find in the Mesozoic and Tertiary a stable list of percentages. The Tertiary figures are much lower than those of the Mesozoic, and would, in fact, require an increase of 600% to bring them to the same magnitude. The Permian percentage in the 1930 column are not quite twice those of the Mesozoic, so that it is perfectly possible that sometime we may have sufficient records to show that the may-flies were relatively more abundant in the Mesozoic than in the Permian. From the standpoint of comparative morphology, however, this is unlikely, for these insects are generally recognized as being the most primitive of any insects now existing. The Mesozoic and Tertiary records of the Blattids are also very constant, and since that of the Mesozoic is far ahead of the one in the Tertiary, we certainly cannot look for a reversal of the present ratios. The figures of all the geological periods point definitely to the conclusion that the cockroaches reached their highest development in the number of species during the Upper Carboniferous, and have been decreasing right down to the present time. Of all our records that of the cockroaches is the least open to radical change. The last order on our list, the Orthoptera, has turned up rather regularly in the various geological formations, and the percentage of the Mesozoic species is so far ahead of either

the Permian or the Tertiary that we are justified in concluding that the order reached its maximum development during the Mesozoic.

For my own part, therefore, I believe that the above percentages, indicating the relative abundance of the species in each order during the several geological periods, is approximately correct for all the orders mentioned, except probably the Neuroptera and Coleoptera. On that basis, at any rate, we may separate the orders into several groups, based upon the time of the maximum development of the order. The Mecoptera, Homoptera, Psocoptera, Plectoptera, and Blattaria are alike in that they had reached their maximum by the Permian. This result is not at all surprising when we reflect that this is precisely what we should expect from the morphology of these insects. For a comparative study of their structure has demonstrated that every one of the orders mentioned is very primitive. It is probable, as I have noted above, that the Neuroptera belong to this series. The next group of orders, those which reached their highest development in the number of species during the Mesozoic, includes the Odonata and the Orthoptera. Here again we find this situation perfectly consistent with the results of comparative morphologists, for these two orders, while primitive in many respects, are a little more highly specialized than those which we have just considered. There remains, then, only a single order, the Diptera, which at present seems to have attained its peak during the Tertiary. And once more we are consistent in our conclusions with those of morphological studies, for the flies are more highly specialized than any of the orders included in the foregoing groups. In this discussion of the development of the insect orders, I have omitted any mention of the Perlaria or stone-flies, because just at present the geological record of these insects is much confused owing to difficulties in interpreting the venation. I have also omitted reference to certain other groups, such as the Heteroptera, Trichoptera, Lepidoptera, Isoptera, and Hymenoptera, none of which has been found in rocks older than the Mesozoic. All these appear to be younger groups, with a shorter and perhaps less completely known geological history than the ones which we have considered. Most of them

seem to have increased in the number of species right up to the present time.

As I bring to a close this discussion of insect paleontology, I cannot resist a feeling of curiosity as to just what discoveries will take place during the next few years, and just how much our present conception of the geological history of the insects will have to be modified by the end of this next decade. I have already ventured to predict above that certain existing orders will some time be found in Carboniferous rocks, and have demonstrated that we must eventually find winged insects in the Lower Carboniferous and probably also in the Devonian. Just how soon this discovery will be made depends upon the coöperation which the entomologists receive from the geologists. For the student of fossil insects is, on the whole, utterly dependent upon the geologists not only to discover but also to collect his specimens. It is impossible to predict whether or not fossil insects will be found in any one deposit; consequently, their discovery can only be made by someone who is already occupied with the study of that particular formation from some geological aspect. And even when a formation is known to contain insects, these fossils are so scarce that usually it is not practical to work the beds for insects alone. Of course there are a few insect-bearing strata, such as the Wellington Shales of Kansas and the Florissant Shales of Colorado, which contain a sufficiently high percentage of insects so that an expedition of that nature is worth while. But these beds are exceptions. It is upon the geologist who is investigating some other aspect of the strata that we must depend for our fossils. For this reason it is particularly deplorable—and I make this statement with all due apologies to the few exceptions—that geologists have not favored us in late years with their needed coöperation. While recently visiting one of the larger eastern universities, I was much astonished to find in the possession of the geological department a splendid wing of a Paleodictyopteran, complete from the apex to the base, and showing every vein with gratifying clearness. The specimen was without locality label, and no one appeared to know just where it was collected; for several years the specimen had been used in the elementary geology class as an example of

a fossil insect, and has passed thru so many inexperienced hands that all its brightness and freshness had gone! Let us therefore hope that the geologist, the paleobotanist, and other paleontologists, will be on the alert for fossil insects, and that once having found them, will place them in the hands of one who can give the fossils the necessary attention. Perhaps this is too much to expect in these days, when the vision of the average geologist is so obscured by petroleum; but by this means alone will we ever locate a Devonian or Mississippian winged insect,—a find which would contribute more to our knowledge of the origin of the class Insecta than any other single discovery.

A SECOND NOTE ON GESOMYRMEX

By William Morton Wheeler[1]

On his recent return from a sojurn of several years in the Philippines, Dr. James W. Chapman generously gave me a considerable portion of a colony of Gesomyrmex which he had had under observation at his camp (alt. 1500 ft.) near Dumaguete. The specimens are of unusual interest because they comprise not only a complete series of the various worker forms and therefore confirm the conclusions recorded in my former paper[2] on the identity of the genera Gesomyrmex and Dimorphomyrmex, but also the mother queen of the colony and an adult male. In the paper cited I endeavored to ascertain the characters of this sex from a young pupa of the Javan G. *kalshoveni* Wheeler, but examination of the specimen from the Philippines proves that my inferences from pupal structure were inadequate. Comparison of Dr. Chapman's queen with the female of *G. luzonensis* Wheeler shows that whereas both belong to the same species, the former represents an undescribed variety. Since the Luzon form is known only from a female specimen I shall have to compare the workers of the new variety with those of the closely allied *kalshoveni.*

Gesomyrmex luzonensis var. **chapmani** var. nov.

Worker maxima.—Length 6.5-7 mm.

Distinctly larger and more robust than the maxima of *G. kalshoveni* and of a deeper, more reddish yellow color, with a large spot on the ocellar region and the discal, or

[1]Contribution from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 332.

[2]The Identity of the Ant Genera Gesomyrmex Mayr and Dimorphomyrmex, Ernest Andre'. Psyche 36, 1929, pp. 1-12, 1 fig.

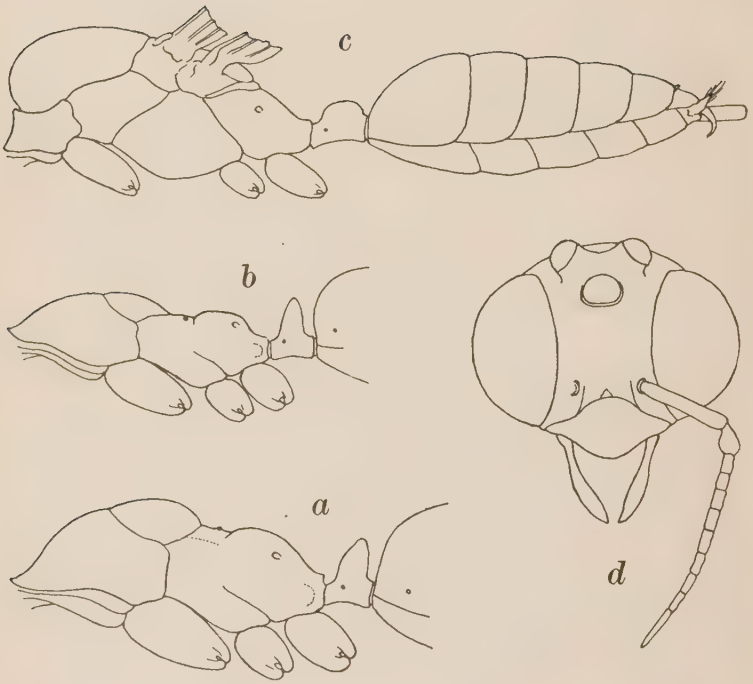

Fig. 1. *Gesomyrmex luzonensis* Wheeler, var. *chapmani*, var. nov. *a*, thorax and petiole of worker maxima in profile; *b*, same of worker minima; *c*, thorax and abdomen of male; *d*, head of male, dorsal view.

central portion, of the pronotum dark brown. In some specimens the pleuræ and epinotum are reddish brown. Basal portions of the several gastric segments distinctly brownish. Mesonotum broader than long and much more convex than in *kalshoveni*. Petiole thicker above and less distinctly cuneate.

Worker media.—Length 4.5-6 mm.

The larger specimens are as large as the maximæ of *kalshoveni* and differ from them only in their deeper yellow coloration, in having the spot on the vertex and the disc of the pronotum brown, though paler than in the maxima, and in the thicker and blunter petiolar node. In the smaller specimens the brown on the vertex and pronotum becomes fainter or disappears altogether.

Worker minima.—Length 2.5-3.5 mm.

Without dark markings and very similar to the minima of *kalshoveni*, but with the petiolar node distinctly thicker, less compressed above and therefore less cuneate in profile. The general yellow color of the body seems to be somewhat darker.

Female (deälated).—Length nearly 9 mm.

Closely resembling the female of *luzonensis* in structure, pilosity and sculpture but differing in coloration. Paler and more ivory yellow, with a large rhomboidal spot on the middle of the head, covering more than the ocellar region, the wing insertions and the discal portions of the pronotum and epinotum dark castaneous brown. Dorsal surface of the same color, with the borders of the segments and a transverse band at the base of the first segment yellow.

Male.—Length 3.6 mm.

Head small, including the large, convex eyes somewhat broader than long, broadly rounded behind, with extremely short cheeks. Ocelli large and prominent. Clypeus somewhat broader than long, convex in the middle, anteriorly

produced as an entire, rounded lobe. Mandibles small, slender, edentate, subspatulate. Frontal area very small, triangular; antennæ short and slender, 11-jointed; scapes cylindrical, nearly as long as the four basal funicular joints together; first funicular joint swollen, ellipsoidal, one and one-half times as long as broad, remainder of funiculus tapering, joints 2-9 subequal, about one and one-half times as long as broad, terminal joint narrower, as long as the two penultimate joints together. Palpi long, maxillary pair 6-jointed, labial pair 4-jointed. Thorax broad and robust anteriorly, gradually narrowed behind, the pronotum short, with raised posterior border; mesonotum broader than long, broader than the head, strongly convex in front and somewhat overhanging the pronotum. Scutellum large, but not very convex. Epinotum small, narrower behind than in front, with rather flat, sloping dorsal surface, without differentiated base and declivity. Petiole resembling that of the female, nearly as long as broad, subrectangular from above, in profile with a thick, broadly and evenly rounded node, and feebly concave ventral surface. Gaster small, slender and elongate; cerci present; genital appendages exserted, the stipites small, spreading, subtriangular, acutely pointed and pilose, the volsellæ slender, falcate and deflected; sagittæ much larger, longer than broad, parallel-sided, with truncated tips. Legs slender; hind femora slightly bowed; tarsal claws large.

Smooth and shining, very indistinctly and finely shagreened.

Pilosity white, delicate, almost absent on the head and thorax; erect and more abundant on the petiole and gaster, especially on the former; appendages with sparse, appressed pubescence; funiculi with short oblique hairs.

Sordid or brownish yellow; head dark brown; mesonotum and scutellum pale brown. Wings yellowish hyaline, with pale yellow veins and pale brown pterostigma.

Described from a series of 43 workers, a single female and single male, all from the same colony, captured by Dr. J. W. Chapman at Dumaguete, Negros Oriental, P. I.

A study of the male of this ant has led me to reverse my opinion in regard to the specimen which Mayr regarded as the male of his *G. hoernesi* from the Baltic Amber. Apart

from its much greater size and its smaller mandibles, petiole and genital appendages, his specimen would, after all, seem to be a true male Gesomyrmex. The head, antennæ, thorax and wings are very much like the corresponding parts of the above-described male of *chapmani*, and the discrepancies in the other parts are perhaps attributable to defects in Mayr's figure. It is not so easy to make an accurate drawing of an insect embedded in a block of fossil resin as it is of one carded or pinned.

The specimens of the new variety were accompanied by Dr. Chapman's notes which are worth quoting, because they contain the first observations on the habits of Gesomyrmex.[1]

"May 11, 1924, at 8 A. M., while sitting on our azoteo, I noticed on the balustrade a honey-colored ant which arrested my attention by its peculiar jerky, zigzag gait and unusually large dark eyes. On capturing it I found it to be a small worker of Gesomyrmex! Then a few others were seen running about in the same place. I smeared some ripe banana in their path on the railing and found that they at once proceeded to gorge themselves with the juices. They eventually moved away and I followed them down a banister and along the sill to one of the large posts which serve as supports of the house. From this post they passed to a pole, which I had placed diagonally between two of the posts, to serve as a brace. They descended this for a foot or more and together entered a hole in its surface. There were other workers within the entrance but they could not be induced to come out. During the day several workers were seen to visit and feed on the banana. The last one retired to the nest at 5 P. M., apparently for the night.

"The pole containing the nest was about eight feet long and was two and one-half inches in diameter where the nest was situated. The entrance consisted of four small, slit-like holes, close together and resembling the orifices of beetle burrows. The pole had been cut about two weeks previously on the mountain side behind the house from a particular

[1]Dr. Chapman also sent me a series of drawings of the various worker castes of *G. chapmani* to illustrate the identity of Gesomyrmex and Dimorphomyrmex. I have not reproduced these drawings because they are so much like those in my paper on *G. kalshoveni*.

tree, which was selected because it is known to be very resistant to the attacks of termites.

"May 12 and 13 the workers continued to visit the ripe banana in small numbers. I failed to excite the colony or to bring out any of the workers by pushing a straw into their nest entrances, by pounding on the pole or blowing into the cavity. On the evening of May 13 I decided to open the nest and therefore placed the pole on a large collecting canvas, filled the entrances with alcohol and carefully split the wood. The four entrances were seen to unite to form a single funnel-like passage, which grew narrower towards the end of the pole and opened into the middle of the main nest-cavity. This was about five inches long and one and a quarter inches from the surface. The two ends of the cavity were rounded out and the wood around the excavated pithy center had been gnawed away to form several irregular galleries. The colony had evidently been nesting in these cavities for some time. The wood was green and solid. There were about 150 adult workers, their queen, male and a number of eggs and larvæ."

These observations antedate and add materially to those of Dr. Kalshoven on *G. kalshoveni* cited in my first note.[1]

We may conclude from them that the colonies of Gesomyrmex are monometrotic, or possess a single mother queen, that they are not very populous and nest in sound wood. Like other lignicolous ants they probably take possession of the abandoned burrows of other insects and enlarge them by tunnelling in the wood as the colony grows. Dr. Chapman's observations show that the smaller and more numerous workers do most of the foraging, have a peculiar, jerky, zigzag gait and are very timid. He has not observed the guarding of the nest-entrances by the largest workers, though he seems to have seen workers stationed just within the entrance gallery.

[1]Note on Gesomyrmex. Psyche, 36, 1929, pp. 91, 92.

TWO NEW GENERA OF ANTS FROM AUSTRALIA AND THE PHILIPPINES

By William Morton Wheeler[1]

Chapmanella gen. nov.

Worker: Integument rather thin, smooth and hairy. Head elongate, high in the frontal region, depressed and narrowed behind, without posterior corners. Eyes very small but distinct, placed well up on the dorsal surface near the middle of the sides. Ocelli absent. Mandibles narrow, decussating, with oblique, dentate apical borders. Clypeus rather large, not extending back between the frontal carinæ, which are very short, poorly developed and not very far apart. Frontal area and groove absent. Palpi short, the labial pair 4-jointed, the maxillary pair apparently 6-jointed, with the terminal joint much shorter than either of the two subequal preceding joints. Antennæ very long and slender, 12-jointed, inserted near the posterior corners of the clypeus; funiculus filiform, scarcely thickened apically. Antennal and clypeal foveæ not confluent. Thorax long and slender, with distinct promesonotal and mesoëpinotal sutures. Anterior portion of mesonotum narrow and subcylindrical; mesosterna convex and somewhat swollen anteriorly. Metanotal spiracles prominent, closely approximated, on the dorsal surface just anterior to the base of the epinotum, which is small, short and unarmed, with its spiracles situated on each side at the angle between the base and declivity. Petiole small and elongate, with a low, erect node at its anterior end. Gaster moderately large, with short first segment, which is convex anteriorly but does not overlie the petiole. Legs

[1]Contribution from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 333.

very long and slender; middle and hind tibiæ without spurs; tarsal claws slender and simple.

Genotype: *Chapmanella negrosensis* sp. nov.

Chapmanella negrosensis sp. nov.

Worker.—Length 4 mm.

Head longer than broad, subelliptical, broadest through the middle where the small eyes, consisting of only about 16

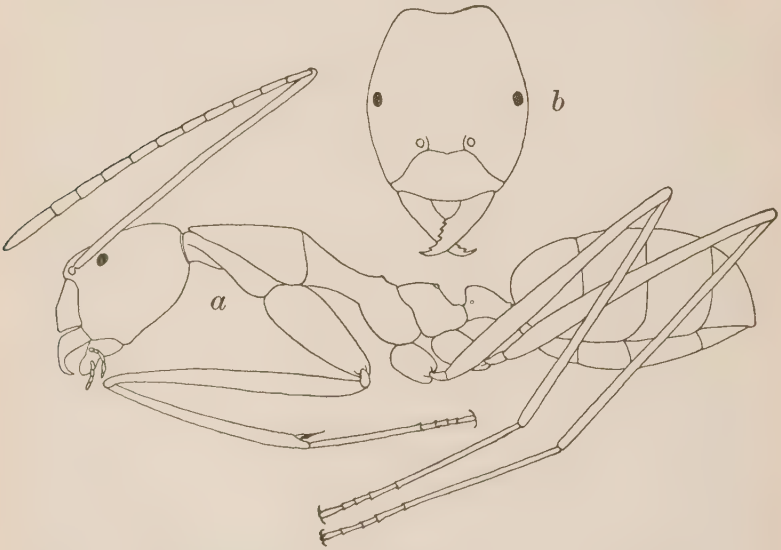

Fig. 1. *Chapmanella negrosensis* gen. et sp. nov. *a*, Worker, in profile; *b*, head of same, dorsal view.

ommatidia, are situated, the occipital border concave. Antennal scapes straight, extending more than half their length beyond the occipital border; all the joints of the funiculus except the last, subequal, nearly three times as long as broad, the last joint somewhat pointed, as long as the two penultimate joints together. Mandibles 6-toothed, the terminal tooth long and curved, the remaining teeth

oblique, subequal, except the third from the apex, which is distinctly smaller. Clypeus convex, bluntly subcarinate in the middle, its anterior border broadly rounded and entire. Pronotum from above elliptical, one and one-half times as long as broad, with evenly rounded sides, its dorsal outline in profile nearly straight and horizontal. Mesonotum as long as the pronotum, its subcylindrical anterior portion long, slightly concave laterally, dorsally and ventrally, descending to the posterior portion which embraces the sides of the epinotum. The projecting metanotal spiracles interrupt the dorsal outline near its posterior end. Mesoëpinotal constriction short and feeble. Epinotum broader than long, in profile with straight base and declivity, meeting at an obtuse angle. Petiole longer than broad, broader in front than behind, the node in profile perpendicularly truncated anteriorly, rounded above, with its posterior surface gradually descending with even convexity to the posterior end of the segment. Legs very long and slender.

Smooth and shining; body, scapes and legs very delicately and indistinctly shagreened, with sparse piligerous punctures; mandibles less shining, very finely punctate-striate.

Pilosity yellowish, bristly, of uneven length, erect and moderately abundant, long on the body, shorter and more oblique but coarse also on the scapes and legs. Pubescence undeveloped.

Yellow, the legs and antennæ scarcely paler; mandibles more reddish with black teeth.

Described from a single specimen taken by Dr. J. W. Chapman, April 7, 1927, at Dumaguete Negros Oriental, Philippine Islands. This specimen, which superficially resembles an *Anoplolepis longipes* Jerdon, formed a portion of the prey captured by an army of *Ænictus læviceps* F. Smith. The remainder of the prey comprised a worker of *Ischnomyrmex longipes* F. Smith, and two workers and several larvæ of *Polyrhachis (Myrma) mayri* Roger. The head of the Chapmanella had been crushed and the tip of its gaster bitten off by its captors, so that the conformation of these regions may be inaccurately represented in the figure.

The genus Chapmanella appears to be most closely related

to Prenolepis and Paratrechina, as redefined by Emery, but is peculiar in the vary small size of the eyes, the short palpi, the unmodified base of the gaster, the shape of the petiole, the extremely long appendages and the absence of spurs on the middle and hind tibiæ. The pale color, small eyes, very long appendages and long pilosity of this ant indicate that it must be hypogaeic in habit. This might explain why it has not been taken heretofore and why the *Ænicti,* which forage more or less subterraneously, were able to reveal its existence.

The following is another undescribed genus belonging to the same tribe (Lasiini) of the subfamily Formicinæ.

Aphantolepis gen. nov.

Worker: Resembling Prenolepis in the structure of the head, thorax and gaster, but with somewhat harder integument. Eyes of moderate size; ocelli absent. Mandibles small, triangular, decussating, with finely dentate apical borders. Clypeus short, not extending back between the frontal carinæ, which are distinct, subparallel and as far apart as their distance from the lateral borders of the head. Frontal area and groove obsolete. Antennæ rather stout, 12-jointed, the funiculi but slightly enlarged towards their tips. Antennal and clypeal foveæ confluent. Palpi long, maxillary pair 6-jointed, with thickened basal and elongate terminal joint; labial pair 4-jointed. Thorax with deep mesoëpinotal constriction, dorsally approximated and protruding spiracles and prominent, highly placed epinotal spiracles. Petiole flattened above, without a node. Gaster rather large, its first segment truncated anteriorly and in life evidently overlying the petiole. Middle and hind tibiæ with well-developed spurs; tarsal claws simple.

Genotype: *Aphantolepis quadricolor* sp. nov.

Aphantolepis quadricolor sp. nov.

Worker—Length 2.7 mm.

Head slightly longer than broad, distinctly narrowed anteriorly, with broadly rounded posterior corners and en-

tire posterior border. Eyes moderately large and convex, placed a little in front of the middle of the sides of the head. Surface of clypeus rather flat, slightly projecting but scarcely subcarinate in the middle, the anterior border transverse, feebly sinuate on each side. Mandibles with nearly straight external and somewhat oblique apical bor-

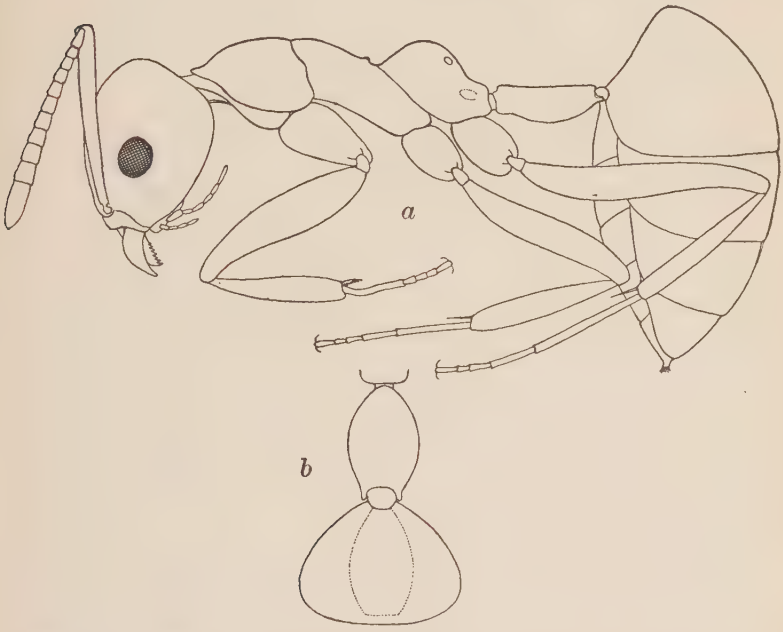

Fig. 2. *Aphantolepis quadricolor* gen. et sp. nov. *a*, Worker, in profile; *b*, petiole and anterior portion of first gastric segment, dorsal view.

ders, the latter with seven small, acute teeth, which are somewhat crowded and subequal, except the basal and third tooth from the apex, which are smaller. Antennal scapes extending nearly one-third their length beyond the posterior border of the head; first funicular joint twice as long as broad, nearly as long as the two succeeding joints together; joints 2-10 only slightly longer than broad, the terminal joint as long as the two penultimate joints together. Pro-

notum from above trapezoidal, broader than long, broader anteriorly than posteriorly, in profile feebly convex above. Mesonotum much narrower than the pronotum, slightly longer than broad, as broad in front as behind, with subparallel, slightly concave sides, in profile rounded and sloping backward to the pronounced mesoëpinotal constriction. Epinotum broader than long, subrectangular from above, slightly broader behind through the prominent spiracles than in front; in profile with very convex, rounded base passing without an angle into the shorter, concave declivity. Petiole small, nearly twice as long as broad, from above regularly elliptical, except at the posterior border where it is excised for the articulation of the gaster. A very feeble trace of the absent node is represented by the narrowly rounded anterior end of the flat dorsal surface; the ventral surface is distinctly convex. Gaster broad anteriorly, rapidly tapering and pointed posteriorly, the anterior truncated surface of the first segment longitudinally impressed in the middle for the accommodation of the petiole. Legs rather stout.

Smooth and shining, especially the dorsal surface of the head, the pronotum and the gaster, meso- and epinotum more subopaque, very finely and densely punctate or reticulate. Mandibles smooth, with a few scattered piligerous punctures.

Erect hairs brownish, pointed, few in number, of unequal length, arranged as pairs of macrochætæ on the head, pro- and mesonotum as in some species of Paratrechina (subgen. Nylanderia). Gaster both dorsally and ventrally with similar but shorter hairs, and the head and gaster also with more numerous short, suberect hairs or coarse pubescence. Antennal scapes and legs with pale, long, oblique, rather abundant pubescence.

Head and thorax yellowish red, the former a little darker, with a fuscous cloud on the vertex. Manibles, petiole, legs, scapes and first funicular joint clear yellow; remaining funicular joints dark brown; mandibular teeth and gaster black; terminal tarsal joints reddish.

Described from a single specimen taken by Mr. A. M. Lea in the Cairns District, Queensland, Australia, "among fallen leaves."

This beautiful little ant may be readily recognized by its very peculiar nodeless petiole, which is unlike that of any known Formicid. In other respects it very closely resembles certain species of Prenolepis and Paratrechina (of the subgen. Euprenolepis). Until the female and male have been discovered it will be difficult to decide whether Aphantolepis is to be regarded as an independent genus or as a subgenus of Paratrechina.

TWO MERMITHERGATES OF ECTATOMMA

By William Morton Wheeler[1]

Since the publication in 1928 of my review of the modifications induced by Mermis parasites in various species of ants, two additional cases have been reported, one by Strelnikov (1928) in a Ponerine ant, *Pachycondyla striata,* from Paraguay, and one by myself (1929) in a Formicine ant, *Camponotus (Tanæmyrmex) punctatus* from Argentina. Two other interesting mermithergates have just come to light among some ants collected by Mr. Nathan Banks and Mr. P. J. Darlington. One of these belongs to the typical *Ectatomma tuberculatum* Olivier, the other to its variety *punctigerum* Emery. As long ago as 1890, Emery (1890 *a*) mentioned a peculiar worker of the typical *E. tuberculatum,* which we now know must have been a mermithergate, but he merely cites it as "analogous" to a similar specimen of *Neoponera villosa* with small head and voluminous abdomen.

The mermithized specimen of the typical *E. tuberculatum* was taken by Mr. Banks on July 15, 1924, near the tropical laboratory on Barro Colorado Island, Panama. It measures nearly 16 mm. and is of the same brownish ferruginous color as normal workers from the same locality, but with the gaster distinctly darker. The head is smaller and narrower, with scarcely an indication of the posterior angles and with very slightly larger and more convex eyes. Ocelli lacking. Antennal scapes extending half their length beyond the posterior corners of the head and the mandibles slightly narrower. Thorax shaped as in the normal worker but slightly less robust, with distinct, blunt teeth on the epinotum. Petiolar node more strongly compressed anteroposteriorly. Postpetiolar and gastric segments, especially

[1]Contribution from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 334.

the first, enlarged and distended with Mermis. Legs decidedly longer than in the normal worker.

Head sculpture peculiar in that the longitudinal rugæ are finer, closer together and decidedly more numerous on the front than in the normal worker. The reticulate rugæ on the sides of the vertex in the latter are also replaced by such longitudinal rugæ. Thoracic sculpture as in the normal worker. Petiolar node transversely rugulose and not irregularly rugose above. Postpetiole and gaster more opaque throughout, finely and densely striate, with a satiny lustre; the striæ transverse and converging behind on the postpetiole, longitudinal on the gastric segments. Venter more shining but very finely and transversely, though more superficially striate throughout. The sculpture of the abdomen therefore resembles that of the normal worker *tuberculatum*. The pilosity of the mermithergate is quite normal.

Although the typical form of *E. tuberculatum* is a common ant over a large portion of the Neotropical Region from Southern Mexico to Southern Brazil, its two varieties, *acrista* Forel and *punctigerum* Emery have a much more restricted distribution. The var. *acrista* is known only from Paraguay; Emery (1890 *b*) described *punctigerum* from a couple of workers taken by Simon at San Esteban, Venezuela. It is certainly the common, if not the only form of the species in Trinidad, where it has been taken by Prof. R. Thaxter and myself, and Dr. George Salt and Mr. Darlington brought me specimens of it from Northern Colombia. The worker differs from that of the typical *tuberculatum* in coloration, being decidedly darker and more brownish, and in the sculpture of the postpetiole and first gastric segment, the coarse, sparse punctures on which are larger, more impressed and interrupt the striated sculpture. Moreover, the striation on the first gastric segment is much feebler than in the typical *tuberculatum* and becomes obsolete on the sides, so that the whole segment is decidedly smoother and more shining. The female *punctigerum* (undescribed) is scarcely paler than the worker, with very similar abdominal sculpture though in some specimens the striation on the first gastric segment is even

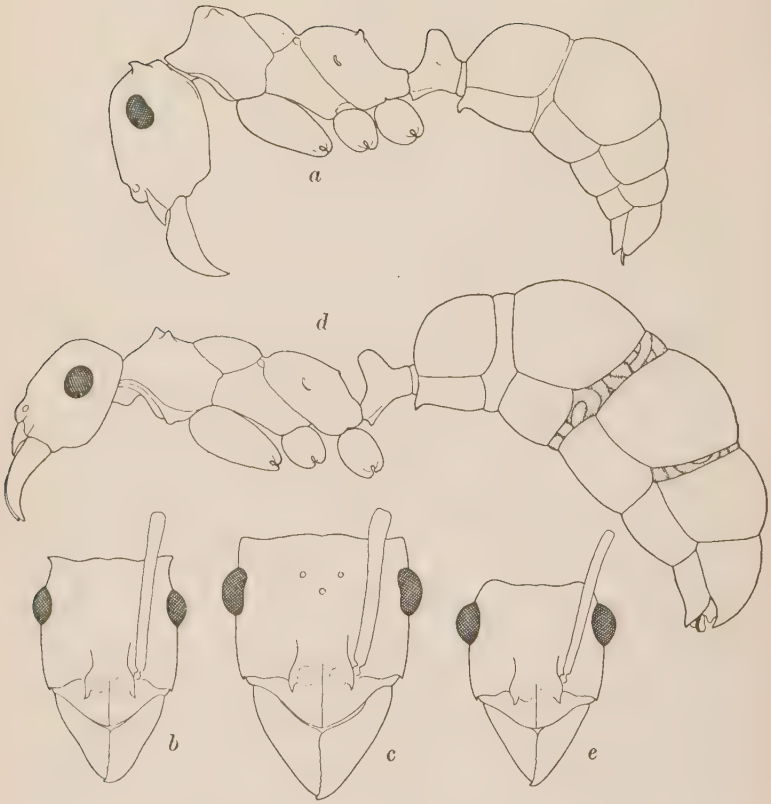

Fig. 1. *Ectatomma tuberculatum* Olivier var. *punctigerum* Emery. *a*, normal worker in profile; *b*, head of same, dorsal view; *c*, head of normal female; *d*, mermithergate in profile; *e*, head of same.

feebler and the surface, therefore, even smoother and more shining.

The *punctigerum* mermithergate (Fig. 1d,e) was captured by Mr. Darlington on April 20, 1920 at St. Augustine, Trinidad, together with three normal workers of the variety. Were it not for this association the specific identity of the parasitized specimen might be doubtful, though its cephalic and thoracic sculpture is clearly of the *E. tuberculatum* type. The specimen measures 16.6 mm. in length and is longer than the average normal worker which measures only about 10-12.5 mm., but the proportions of the head, thorax and abdomen are very different. In the mermithergate the head measures only 3.2 mm. in length, including the mandibles, the thorax 4 mm., the abdomen 9.4 mm. The corresponding measurements of the normal large worker are: head 3.5 mm., thorax 4.5 mm., abdomen 4.5 mm. Though the head and thorax resemble those of the normal worker they are therefore decidedly smaller and more slender. The head, excluding the mandibles, is nearly square, very slightly longer than broad, with very feebly rounded sides and the posterior angles merely rounded-rectangular and not sharply rectangular or even distinctly cornuate as in the normal worker. Eyes larger, more protuberant, nearly hemispherical. There are no traces of ocelli. Antennal scapes extending nearly half their length beyond the posterior corners of the head (only two-fifths in the normal worker), mandibles somewhat narrower. Besides its smaller and more slender dimensions the thorax differs from that of the normal worker in having the lateral tubercles of the pronotum more acute and less auriculate, the median tubercle or projection narrower and more sharply defined. The base and declivity of the epinotum form a less distinct obtuse angle and the epinotal teeth are reduced to mere denticles. Petiole very similar to that of the normal worker but the node slightly more compressed anteroposteriorly. Postpetiole and gaster much larger and more voluminous, owing to their containing a large Mermis, the compact coils of which are visible through the distended intersegmental membranes. The hypertrophy affects not only the postpetiole and first gastric segment but also the deflected second, third and fourth gastric segments,

which in the normal worker and even in the female are much shorter and telescoped into one another. Anteroventral projection of the postpetiole less developed than in the normal worker and female; legs as long as those of the former.

Sculpture peculiar; the longitudinal rugæ on the front and vertex decidedly less coarse, denser and more numerous than in the normal worker, with the reticulate rugæ between the front and eyes also much finer; rugules on the median portion of the clypeus more numerous; striæ on the mandibles somewhat coarser. On the thorax the rugæ are distinctly finer and more definitely transverse; those on the posterior portion of the pronotum also transverse, not coarse and irregular as in the normal worker. The rugæ on the petiolar node are finer and symmetrical. On the postpetiole and gaster the sculpture is quite unlike that of *E. tuberculatum* and much like that of *E. quadridens* Fabr., the tergites of all the segments being finely and regularly striate, so that the surface is subopaque, with a faint satiny lustre. The striæ on the postpetiole are arcuate anteriorly, longitudinal in the middle and transverse posteriorly; on the first gastric segment longitudinal anteriorly and transverse behind; on the second and third gastric segments transverse and more oblique on the sides. The fourth segment is more shining, with finer and less distinct striæ. The coarse punctures on the postpetiole and first gastric segment are small, inconspicuous and scattered, as in *E. quadridens* and therefore very different from those of *punctigerum* or the typical *tuberculatum*.

Pilosity as in the normal *punctigerum* worker, but less abundant, especially on the abdomen.

Coloration decidedly darker; dark brown, almost blackish, with brownish yellow clypeus and mandibles, the former streaked with fuscous in the middle, the latter fuscous externally. Femora, terminal tarsal joints, tips of scapes, apical halves of antennal funiculi and borders of gastric segments reddish brown; a spot on the middorsal region of the postpetiole and one on the corresponding region of the first gastric-segment more yellowish.

The specimens described in the preceding paragraphs are obviously modified workers, without any perceptible female

(queen) characters. Even the enlargement of the abdomen is quite unlike that of the normal Ectatomma female, since in this caste the gaster is shaped like that of the worker, though more voluminous, especially in the region of the postpetiole and first gastric segment. The mermithergates are interesting for two reasons, first, because they so clearly illustrate the compensatory decrease in the size of the head and, in Darlington's specimen, also of the thorax as a result of the hypertrophy of the abdomen, which harbors the Mermis, and second, on account of their close resemblance in coloration, abdominal sculpture, and, I may add, also in the shape of the posterior portion of the head, to another species of the same genus, *E. quadridens*. This singular resemblance may, I believe, be most readily explained on the supposition that the specific characters of *quadridens* are probably more nearly those of the ancestral species of Ectatomma and that in the mermithized specimens these characters have been activated as a result of metabolic disturbances set up during metamorphosis by the parasite. To have produced such a pronounced effect on the characters of the adult ant, the young nematode must have entered its body cavity during the larval stage. Recently Vandel (1927) has maintained that in *Pheidole pallidula* infection of the prepupa by the Mermis is sufficient to produce a mermithergate, but his evidence for this contention is very meager. I have called attention to the fact (1928) that the larvæ of the Ponerinæ and Formiciæ (Lasius) spin cocoons before the prepupal stage and that it is therefore very improbable that the young nematode would wait to bore through a tough envelope when it could so easily and directly enter the unprotected, thin-skinned larva. That this is actually what happens, has been shown by Dr. N. A. Cobb, our well-known authority on the nematodes, who writes me that he has found the larva of *Allomermis myrmecophila* Bayliss—"in the body cavity of a queen grub of the dark-colored Lasius from Falmouth, *Lasius niger neoniger*." Falmouth, Massachusetts, is the locality in which Dr. A. H. Sturtevant found the many mermithized queens (mermithogynes) of Lasius described in my paper of 1928.

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A NEW PARASITIC CREMATOGASTER FROM INDIANA

By William Morton Wheeler [1]

For many years I have suspected that some of the species of the huge, cosmopolitan ant-genus Crematogaster might prove to be social parasites. My grounds for this suspicion were the fact that one common Neotropical form, *C.* (*Orthocrema*) *limata* F. Smith subsp. *parabiotica* Forel commonly lives in parabiosis with *Camponotus* (*Myrmothrix*) *femoratus* Fabr. and *Dolichoderus* (*Monacis*) *parabioticus* Forel, and the fact that the females of certain subgenera, notably those of Crematogaster *sens. str.* (as shown in the type of the genus, *C. acuta* Fabr.), Nematocrema and Atopogyne, have small subtriangular gasters like those of the workers and unlike the voluminous, suboblong gasters of the females in other subgenera. This small size and worker-like aspect of the female gaster is, of course, a sign of underdevelopment of the ovaries and an indication that the female may be parasitic, or in other words, adapted to invading and securing adoption in a flourishing colony of some allied species in order to provide for the maturation of her ovarian eggs and the rearing of her offspring.

That a parasitic Crematogaster has probably been found at last, not in the tropics but in our own country, is suggested by a study of some specimens sent me for identification by Professor C. H. Kennedy. They comprise 43 workers and 7 black winged females which undoubtedly belong to a form of our common acrobat ant, *Crematogaster* (*Acrocoelia*) *lineolata* Say (near var. *cerasi* Fitch, but darker), together with 14 females and six males of a distinctly different species. The females of the latter are very small and have the head, thorax and pedicel red as in the

[1]Contribution from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 335.

subsp. *laeviuscula* Mayr (with the vars. *clara* Mayr and *californica* Emery) common in the Gulf States and California. The six males seem to be cospecific with the small females, since their wings are of the same color and also like those of *laeviuscula*. All the forms cited above were taken Sept. 22, 1929 in Robinson Park, Fort Wayne, Indiana, by Professor Kennedy from the same nest, which, he says (*in litt.*) "was large and under the loose bark of a cottonwood log. It contained workers, males, large brownish-black queens and *many smaller shining red and black queens*. These latter queens were a shining cherry red and a pitch black in life and acted differently from the ordinary queens. My memory is that they were more active. They were so different that I cannot believe they are the same species."

The specimens and Professor Kennedy's notes suggest the following reflections:

1. The colony might be said to represent a distinct and hitherto unknown variety of *C. lineolata*, characterized by having dimorphic, or A— and B— females, like *Lasius (Acanthomyops) latipes* Walsh of North America and *L.* (*Dendrolasius*) *spathepus* of Japan. This is very improbable, if, as I believe, the males belong to the small red and black females.

2. It is much more probable that these females and the males represent a distinct species parasitic in a flourishing *C. lineolata* colony, but this again suggests the question as to whether the parasite possesses a worker caste or is workerless like such ants as *Anergates, Anergatides, Epoecus* and *Wheeleriella*.

3. The absence of any workers other than those of the common *lineolata* in the material examined strongly indicates that the parasitic species is represented only by females and males, as in the genera just mentioned.

4. If this interpretation is adopted we must suppose that the parasitic Crematogaster is phylogenetically a comparatively recent off-shoot of the host species, *lineolata*, because its morphological modifications are so feeble. In this respect it resembles such perma-

nent social parasites as *Vespa austriaca* and *arctica* among wasps, the species of the genus Psithyrus among bumble bees and those of the genera Wheeleriella and Epoecus among ants, rather than Anergates and Anergatides, in which the modifications due to parasitism are so considerable.

5. There is only one consideration that would seem to cast doubt on the interpretion of the small red and black females and their males as workerless parasites and that is the presence of perfectly developed virgin *lineolata* females in the same nest, because we should expect the mother queen of the host colony to have been eliminated just after the intrusion of the parasite and hence to have been incapable of leaving either female or worker offspring. It is conceivable, however, either that the mother queen of the new Crematogaster may manage to secure her own adoption and the rearing of her offspring in the *lineolata* colony without supplanting its mother queen, or that the suppression of the latter may be greatly delayed and the rearing to maturity of her female offspring be permitted by the worker personnel.

6. That the small red and black females are parasites and are fertilized in the nest (as in *Anergates atratulus,* though this form has wingless, pupa-like males, so that a marriage flight is out of the question) is indicated by the fact that the 14 specimens are in part winged and in part wholly or partially deälated, whereas the seven females of *lineolata* show no indications of losing their wings. And though Miss A. M. Fielde found that mating may take place in the nest in our common *lineolata,* the conditions in Professor Kennedy's colony suggest that the red and black females are more precocious than the winged females of their host. The differences in the behavior of the two kinds of females, noticed by Professor Kennedy, are also very suggestive in this connection.

As shown in the following description, the female of the new Crematogaster may be readily distinguished from the

female of *lineolata* or of any of its various subspecies and varieties, but the male has departed so little from that of its host, that its characters are rather elusive. This is not surprising since the male is the conservative sex among the Formicidæ.

Crematogaster (Acrocoelia) kennedyi sp. nov.

Female.—Length 5-6 mm.; forewing 5 mm.

Decidedly smaller than the females of *lineolata,* its subspecies *laeviuscula* Mayr, *coarctata* Mayr, *etc.*, which measure 8-9 mm., with the anterior wings 7-7.5 mm. Head less narrowed anteriorly and more rectangular, owing to the sides being straight and the posterior corners less rounded. Antennæ longer, the scapes extending a distance equal to their greatest diameter beyond the posterior corners (not reaching the posterior corners in *lineolata*). Thorax shorter and stouter, the mesonotum being nearly as broad as long (decidedly longer than broad in *lineolata*), the epinotal spines more acute and acuminate, and the base of the epinotum external to the spines conspicuously swollen. Dorsal surface of petiole more convex, with straight instead of concave anterior border, its sides less converging posteriorly; postpetiole more broadly grooved or impressed in the middle behind. Gaster much shorter in proportion to its width, less parallel-sided, more subtriangular and therefore more like that of the worker *lineolata.* Legs rather short.

Even smoother and more shining than the subsp. *laeviuscula.* Mandibles coarsely striato-punctate. Head very finely striated anteriorly, rather sparsely and finely punctate behind; thorax and gaster with similar but even sparser punctures; mesopleuræ and sides of epinotum less shining than the mesonotum, scutellum, postpetiole and gaster, longitudinally rugulose; petiole subopaque, very finely granular. Antennal scapes and legs distinctly punctate.

Hairs glistening, yellowish, erect or suberect, much more abundant, much shorter and of much more even length on the head, thorax and gaster than in *lineolata,* and conspicuously long and abundant on the petiole and postpetiole.

Hairs on the scapes and legs slightly longer and less appressed than in *lineolata.*

Head, thorax, pedicel, coxæ and femora and more or less of the venter of the first gastric segment bright yellowish red, more vivid than in the female of the var. *clara* Mayr of the subsp. *laeviuscula.* Gaster scutellum, metanotum and three large elongate spots on the metanotum, one anteromedian, the others parapsidal, jet black; mandibles, antennæ, tibiæ, knees and tarsi darker and more brownish red; bases and sometimes the whole of the scapes, the tips of the funicular clubs, the ventral portions of the mesosterna, the inner border of each ocellus and the posterior corners of the head, more or less blackened or infuscated. Wings whitish hyaline, the pterostigma and anterior veins of the forewings very faintly yellowish, the remaining veins colorless.

Male.—Length 4 mm.

Very similar to the male of *lineolata* but somewhat more slender; gaster, especially, much narrower and more elongate. Mandibles more linear and narrower, furnished with three more distinctly equal denticles. Funicular joints apparently a little more cylindrical and less monillate. Pronotum distinctly less convex anteriorly and less overarching the pronotum. Epinotum more rounded with less distinct base and declivity and no indications of teeth, except in one of the six specimens.

Somewhat smoother and more shining than the male of *lineolata* and more like that of *laeviuscula.* Mesonotum very finely and rather indistinctly striated and sparsely punctate.

Hairs whitish, almost lacking on the head, thorax and gaster, where they are present, though sparse, in *lineolata;* gaster and legs merely with short, sparse, appressed pubescence; antennæ and genital appendages with short, erect or suberect, very dense white pubescence.

Jet black; mandibles, gaster, antennæ, legs and alar insertions dark brown. Wings whitish hyaline with the pterostigma and anterior veins of forewings even more feebly

tinged with yellowish than in the female; remaining veins colorless.

In conclusion I would suggest that those who encounter flourishing colonies of our common *C. lineolata,* especially during the late summer, scrutinize their various castes with great care and, in the event of again finding the small red and black females of *C. kennedyi,* keep them in artificial nests and observe their adoptive behavior in uninfested colonies of *lineolata* with and without their mother queens.

AN UNUSUAL NEST OF POGONOMYRMEX[1]

By George S. Tulloch

During 1919 Professor Harlow Shapley, while collecting in the vicinity of Pasadena, California, discovered a nest of *Pogonomyrmex californicus* Buckley in which a large number of the worker-like forms possessed vestiges of wings. Professor Shapley noted this unusual occurrence of workers possessing vestigial wings (1920, 1921) and considered them to be pterergates following the term suggested by Dr. Wheeler (1903). Of 1737 worker-like forms taken from this nest during 1919 and 1920, 740 were found to possess vestigial anterior wings or the stubs of broken fore wings. Four ants were noted which possessed vestiges of both fore and hind wings—"a phenomenon not heretofore recorded, as only anterior wings are represented in all other pterergates." There appeared to be no obvious reason why this particular nest should present such an anomalous condition as the intermittent war with the Argentine ant (*Iridomyrmex humilis Mayr*) which has been introduced there, was no more severe for these ants than those of neighboring colonies of the same species. It was noted, however, that this nest had little access to wild barley and similar grasses which is a common food of the species, yet it was well provisioned with mixed grains from a nearby feed store whenever the Argentine ants permitted the nest to be opened for normal harvesting activities. An examination of several thousand individuals from fifty colonies within a radius of two miles yielded only one pterergate.

While engaged in a study of the Formicoid thorax, Dr. Wheeler suggested that the writer communicate with Professor Shapley and ask permission to examine specimens

[1]Contribution from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 328.

from this interesting nest. Professor Shapley kindly gave the writer specimens of the different forms and in conversation described the region in which the nest was found. The writer wishes to thank Professor Shapley for these abnormal specimens and for numerous facts concerning these ants in the locality of Pasadena, California. To Dr. Wheeler the writer wishes to express his thanks for his opinions concerning the specimens.

According to Creighton (1928) abnormalities in ants appear to fall into three fairly well defined categories:

1. Sex mosaics and intersexes.[2]
2. Aberrant forms produced through altered food supply.
3. Freaks and atavistic forms.

The first group includes the various lateral mosaics as well as the rarer antero-posterior type. The second group includes a large number of peculiar forms which arise from pronounced nutritional irregularities. Lack of food may produce dwarf individuals, while loss of food due to the presence of parasites gives rise to pseudogynes. In the event of an overabundance of food, unusually large males and females, egg-laying workers and, more rarely, repletes may result. In the third group may be included those individuals which show duplication, loss or malformation of parts and atavistic forms.

The method by which aberrant forms, particularly pseudogynes, may be produced through altered food supply has been studied by Wasman for more than thirty years. He has suggested the following hypotheses.

1. Ants of colonies, having their larval broods devoured by the *Lomechusa* larvæ try to transmute into workers some larvæ which have already developed somewhat along the path terminating in the queen phase. These efforts result in the production of forms that belong to neither caste.

[2]Intersexes should probably fall in the second category, as recent works indicate that they are produced through a change in the rate of metabolism.

2. Pseudogynes may arise without any effort at transmutation but from female larvæ that have been merely neglected and left unfed after they have passed the stage at which such treatment would lead to the formation of workers. "That the pseudogynes are not the result of pathogenic conditions in the egg or mother queen has been proved experimentally by Viehmeyer (1904) who removed an aged *sanguinea* queen from a colony that for years had been producing pseudogynes, owing to the presence of *Lomechusa* larvæ and caused her to be adopted by a new set of unusually healthy workers from an uninfested colony. Under the changed conditions her eggs developed into larvæ that gave rise to perfectly normal workers" (Wheeler, 1910). It would appear, therefore, that pseudogynes result from an upset in the nutritional balance due to the presence of parasites, although it is impossible to state positively whether they are transmuted females or over-developed workers.

The pterergate falls into the third group of abnormal ants, i. e. freaks and atavistic forms. As there are only a few cases of such forms on record (nine prior to 1920) their sporadic appearance would indicate that they are extremely unusual and thus may be classified in the third category. Dewitz (1878) has shown that in *Formica* the embryonic vestiges of wings are retained until the larval and pupal stages, and it is not surprising, therefore, that we should occasionally find some workers which retain them until the adult stage. No doubt this phenomenon occurs more often than has been suspected, and the minute vestiges are broken off during emergence from the pupal case, or during the mutual stroking of their bodies with their antennæ, to which the ants devote so much of their time. Since the retention of a character that usually disappears among the normal forms is in the broad sense of the term a freak, pterergates or workers possessing vestiges of wings, though in other characteristics exactly like the true worker, fall readily into the third group of abnormal ants suggested by Creighton.

The difference between pseudogynes and workers is very distinct when a large series of forms is available for study, and many comparisons may be made between them. The

pseudogyne is characterized by an enlarged mesonotum and oftentimes by the presence of vestigial wings. It is more robust than the worker, and in the case of some forms retains the median ocellus which entirely disappears in the worker. However, a very complete series of intergrades may be noted, and in some cases a pseudogyne so nearly approximates a worker in size and in shape that a careful examination is necessary to differentiate between them. Pterergates and pseudogynes are easily distinguishable. In the case of a wingless pseudogyne and a pterergate, the distinction is obvious. In the case of a winged pseudogyne and a pterergate, the difference is one of size and structure of the thorax. Usually in winged pseudogynes the lower intergrades tend to lose their wings as they become reduced in size, so that the less developed individuals differ only in size from the worker and from the pterergates both in size and the absence of wings.

From the foregoing discussion of the polymorphic forms of the female ant, it may be noted that the distinctions between the forms are based mainly upon thoracic characters. The thorax of the female ants is as specialized as any that may be found among the winged insects, while the thorax of the worker ants is the most highly specialized, and at the same time as simplified as may be found among all insects. Adlerz has stated in his Myrmecologiska Studier that "we know that those characteristics that distinguish the typical worker from the queen are partly of a retrogressive nature; for example, the reduction of the receptaculum seminis, ovaries, eyes, wings, together with their muscles and muscular attachments, and partly progressive, for example, the increased size of mandibles and their muscles." The adoption of a terrestrial habit and the subsequent disappearance of wings has resulted in a fusion of sclerites in the thoracic region which makes a homological study almost impossible. Usually the dimorphic forms, the winged sexual forms and the wingless workers, are the only forms available for study, the intermediate forms having disappeared during phylogeny. Occasionally intermediate forms appear, giving convenient graduations from the winged to the wingless state, showing how the fusion of the sclerites and the simplification of the thorax may have taken place. In the

material received from Professor Shapley a very interesting series of pseudogynes was noted.[3] Since this series may be of significance in tracing the evolution of the wingless worker from the winged form, this description is offered.

The typical female of *P. californicus* Buckley is rather a large form (Fig. 1, A) about 8-9 mm. in length. It is much larger than the workers and pseudogynes, the difference in size being most noticeable in the thorax and gaster. The thorax is of the typical Myrmicine type, being characterized by the presence of a large parascutellar region on either side of the mesonotum and by the absence of a distinct metathoracic spiracle. In the mesonotum the prescutum is fused with the scutum. The notauli are absent and the parapsidal furrows extend but a short distance forward from the transcutual suture. The lateral and sternal sclerites of the mesothorax are fused and modified so as to make their identification rather difficult. In the mesopleuron the epimeron persists as a narrow region bordering the postero-dorsal margin of the episternum. The episternum is secondly divided into an upper (anepisternum) and lower (katepisternum) plate. The metanotum is reduced to a transverse plate and the metapleuron is almost indistinguishably fused with the propodeum.

The modifications noted in the series selected for study are as follows. Fig. B is a lateral view of one of the larger winged pseudogynes. In this form fusion of the sclerites in the notal region has taken place although the mesonotal region is still enlarged, while the mesopleural region is practically unchanged except for a reduction in size. Vestigial wings and poorly developed tegulæ are present. The metanotum persists as a transverse plate almost indistinguishably fused with the mesonotum and propodeum. In the form next to the true worker (Fig. C) fusion of the pleural region as well as the notal region has taken place, yet the pronotum is still separated from the enlarged mesonotum, the promesontal suture persisting in its entirety. In pseudogynes similar to this one vestigial

[3]Shapley considered these forms to be pterergates, but a comparison of a large number with the typical worker shows them to be pseudogynes.

wings were noted (textfigure). The thorax of the true worker (Fig. C) is one of the most specialized found among the ants. The mesonotum is reduced in size and the sclerites

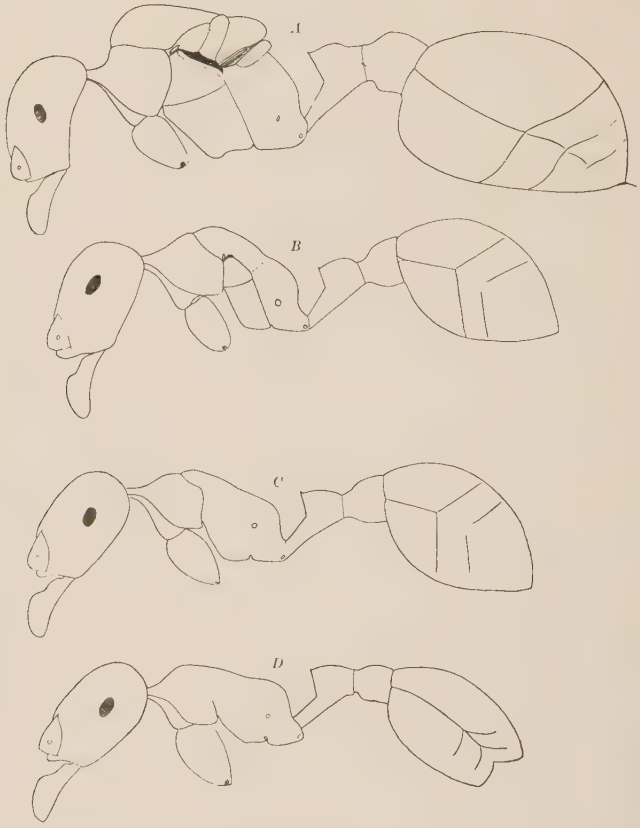

Fig. 1. *A*, Queen of *P. californicus* with wings removed; *B* and *C*, pseudogynes of *P. californicus; D*, worker of *P. californicus.*

have fused together, except the lateral region of the pronotum with the mesopleuron.

In order to comprehend the significance of this series, it is necessary to consider the manner in which a wing

bearing segment may have been evolved from a wingless segment. Snodgrass (1926) has suggested that the insect's ancestor may have been a soft-bodied, segmented animal, resembling in its segmentation the soft-bodied larvæ of some modern insects. Modern adult arthropods, unlike their hypothetical ancestors, have the thorax modified as the locomotor region of the body, and are in general hard-shelled forms, having developed an external skeleton formed of calcareous or chitinous matter, and the hardening of the body wall has had a profound influence on the structure of the segments and on the general mechanism of the animal. The skeletal deposits have taken the form of segmental plates, of which the principal is a dorsal, or tergum and a ventral, or sternum. These two plates are separated on the sides of the segment by a membranous pleural area. The condition found in a wingless thoracic segment is fundamentally of this structure, except that a chitinous pleural plate is present and connected to the tergum and sternum by membranous regions. In the winged thoracic segment these plates have become modified to strengthen the thorax in order to provide solid attachment points for the muscles of the wings. This has come about by the formation of chitinous antecoxal and postcoxal bridges connecting the pleuron and sternum, as well as prealar and postalar bridges connecting the pleuron and tergum. The tergum has become secondarily divided to provide muscle attachment points. Thus the transition from the wingless thoracic segment to the winged segment has been one of strengthening the thorax to accommodate the muscle stresses concomitant with the acquisition of wings.

The embryonic history of insects substantiates the fact that the thorax was first differentiated as the locomotor region of the body by a specialization of three pairs of segmented appendages as the principal organs of progression, this being accomplished by the modification of the gnathal appendages to feeding organs and by the suppression of most of the abdominal appendages. Flight being a comparatively recent development as a further mode of progression, the development of wings and the perfection of the mechanism meant a further and much greater alternation in the structure of the wing-bearing segment than

that which was evolved to accommodate the legs. With a return to a terrestrial environment it is natural to expect that the character most recently acquired should be the first to disappear. In the series of intermediate forms of *Pogonomyrmex* from queen to worker this is precisely what has happened. The appearance of functionless wings, the reduction in the size of the thorax due to the reduction in size of the wing muscles, and the simplification of the mesonotal region presents a stage in the evolution of the apterous forms from the winged forms. This progressive reduction in size of the thorax and wings, and the simplification of the pleural as well as the notal regions represents a recessive stage in the evolutionary series. The loss of vestigial wings and a progressive reduction in size represents a further step, and the true worker type marks the culmination of a long series of evolutionary stages from the winged to the apterous condition. Usually the intermediate forms have disappeared, and only the first and final stages are present, but occasionally abnormal forms such as these persist and give us a convenient series of connecting forms. Moreover, one is not compelled to formulate any hypotheses or construct any hypothetical figures as has been done in the case of the evolutionary stages from the wingless ancestors to the winged insects; here we have living examples of the connecting stages, a condition which is not usually met with in evolutionary study. The writer is very fortunate in having at his disposal these connecting links in most of the subfamilies of the ants. These series will be considered in a later and more comprehensive paper.

The wings of the queen and winged pseudogynes are illustrated in the textfigure. The wing of the queen is about 6 mm. in length and is much reduced in the distal region (Fig. a). The venation of the wing of the first pseudogyne is much reduced, especially in the anal and cubital region. The vestiges in forms similar to Fig. C consist of a small veinless wing sac. The grouping of the winged intermediate forms roughly in order of the development of vestiges by Shapley follows:

With minute veinless wing-sacs, or with stubs of broken wings—385.

With sacs from 0.5 to 1.0 long and indistinct veining—219.

With transparent, clearly veined winglets from 0.8-1.5 —132.

He further states that "the gradation of wing vestiges is, however, perfectly continuous, from small protuberances (without appendages) on the mesothoracic segment to the most developed winglets, with venation approaching that

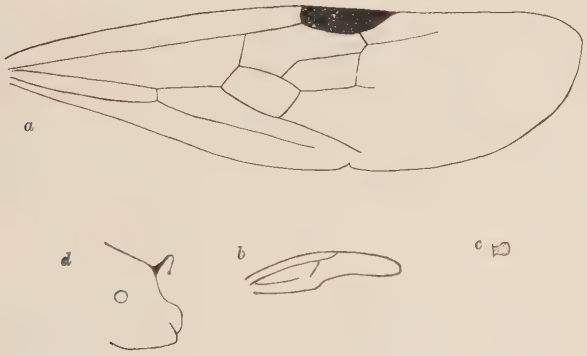

Fig. 2. *a,* wing of queen of *Pogonomyrmex californicus,* Buckley; *b,* wing of pseudogyne shown in Fig. 1, B; *c,* wing of pseudogyne shown in Fig. 1, C; *d,* propodeum of pseudogyne.

of the wing (6 mm. in length) of the mature queen." Brues (1903) distinguishes three types of vestigial wings:

1. Wings having essentially a pupal character, viz, developing as normal wings up to the pupal stage, but failing to expand.

2. Wings essentially normal except for their similar size and less complex venation.

3. Wings consisting of little more than a hollow bag and giving no clue from their appearance as to the probable wing structure of their ancestors.

The vestigial wing (Fig. b) from the first pseudogyne of the series would fall into the second category, while the

sac-like vestige (Fig. c) of a wing from forms similar to Fig. c would fall into the third group. The third group apparently represents the stage just preceding total aptery and is, therefore, phylogenetically, the most recent condition.

In addition to the pseudogynes found in this nest another interesting group of four specimens was noted. These were supposedly workers possessing vestiges of both fore and hind wings. On examining a specimen of this form the writer finds it to be a deälated female, the stubs of wings giving the impression of vestigial wings. However, this particular specimen is extremely interesting from another point of view, as it possesses a propodeal spine on the right side of the body and none on the left. (Fig. d) Since spines do not occur on this particular species this specimen may be classified as a freak, since it is probably an atavistic form.

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NOTES ON *EUPONERA GILVA* (ROGER) (HYMENOPTERA, FORMICIDAE)

By Wm. S. Creighton and George S. Tulloch[1]

In a collection of ants made by the senior author in Alabama during the months of May and June, 1929, there are many specimens of *E. gilva* (Roger). These are of interest both because of the presence of sexual forms, which have not been previously described, and also because of their bearing on the subspecies *harnedi,* recently described by M. R. Smith. The total number of specimens secured was about three hundred. Most of these came from one unusually large nest found at Point Clear, Baldwin County. Others were taken at Spring Hill (Mobile), and a very interesting nest containing five deälated females was discovered near Florence. It would appear that *gilva* is by no means as rare as was formerly supposed. Its scarcity in collections may be ascribed to the combination of a restricted type of nesting site and a southern range which has kept it out of the hands of collectors. It prefers to nest under the bark of fallen pine trees, selecting trees which are lying in such a position that the trunk is clear of the ground for at least a part of its length. The nests are made in the thin and rather spongy layer between the bark and the wood and always on the under side of the trunk. This insures an abundant supply of moisture, which is apparently indispensable to these insects. With the single exception noted above, all the colonies found were small. Many males, a single winged and somewhat callow female and much well-developed brood came from the Point Clear colony which was taken June 20.

E. gilva was originally described by Roger in 1863. Emery in 1895 corrected and amplified the description and

[1]Contribution from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 329.

figured the thorax. Wheeler and Gaige in 1920 redescribed the insect from specimens taken at Camden, Tennessee. Unfortunately the figure which was to accompany the description was omitted in publication. In 1929 M. R. Smith erected a new subspecies which he called *harnedi*. The types of this insect were found at Columbus, Mississippi. The paper containing the account of this subspecies was received while the present work was in preparation. From certain remarks made by Dr. Smith in his introduction, it was apparent that some mistake had been made in regard to the cotypes of *harnedi*. These were supposed to have been examined by Dr. Wheeler, but upon inquiry the single specimen from the type series present in his collection proved to be a female. Under such conditions it was manifestly impossible that any opinion of the status of the worker could have come from Dr. Wheeler. Furthermore this female of *harnedi* was so similar to those of the typical *gilva* taken by the senior author that the validity of *harnedi* seemed very questionable. To clear up the matter cotypes of *harnedi* were secured through the coöperation of Dr. Smith. The authors are glad to take this opportunity to thank him for the gift of these specimens and also for his consideration in laying aside his own description of the sexual forms, which was in course of preparation at the time when he learned of this paper.

A comparison of the cotypes of *harnedi* with specimens which we regard as the typical *gilva* has convinced us that the former must be regarded as a synonym. The two insects are identical as to the width of the head, the length of the antennal scapes and the size of the eyes. The specimens of *harnedi* are as robust as those of *gilva* and their size is well within the range shown by the latter. In coloration Dr. Smith's specimens are identical with the darker specimens taken in the Point Clear colony, the thorax being practically as dark as the head, and the appendages a rather dingy brownish yellow. This condition is apparently shown by the older individuals in the colony, since there are many specimens from the same nest in which the thorax is somewhat lighter than the head and the appendages are of a clear brownish yellow. We were unable to detect any significant difference in the sculpture of the two, although

the pronotum and mesonotum of *harnedi* appeared a trifle more glabrous than that of some of the specimens of the typical *gilva*. The abdominal pilosity of *harnedi* also seemed slightly longer and more abundant, but here again it was impossible to make a satisfactory distinction because of the variability of the typical form. We are of the opinion that the minor differences shown by *harnedi* are those which have been used to distinguish the so-called nest variety. To establish varietal status on this basis necessitates the frequent splitting of a series from a single colony, a procedure which we consider taxonomically unsound. The authors feel sure that Dr. Smith will agree that synonymy is preferable to the use of such minute distinctions.

It may be of interest to note here that the name *gilva* appears to have been a misnomer. As ordinarily used *gilva* refers to the light yellow color more often characterized by the term *flavus* or *flava*. The name *gilva*, therefore, seems scarcely applicable to the ferrugineous specimens which have been found to represent this form, and one is justified in questioning that our present material is of the same color as Roger's types. That the latter were also ferrugineous is indicated by Emery's statement in his description of '95. Emery had for study two workers from the Berlin Museum. Although these do not seem to have been cotypes, they were, in all probability, compared with Roger's original specimens. Emery notes that their color is much darker than that of the European *ochracea*. There are two specimens of *ochracea*, taken by Emery, in the collection of Dr. Wheeler. The color of these is a clear, golden yellow, notably lighter than that of any specimen of *gilva* which we have seen. We may consequently conclude that the color of Emery's specimens of *gilva*, and presumably Roger's also, was the same as that of our present material.

Descriptions of the sexual forms of *E. gilva* and figures of all three casts are presented below:

Euponera (Trachymesopus) gilva (Roger)

Ponera gilva,

Roger, Berl. Ent. Zeitschr., Vol. 5, p. 170, (1863).
Mayr, Verh. Zool-bot. Ges. Wien, Vol. 36, p. 438, (1886)

Dalla Torre, Cat. Hymenop., Vol. 7, p. 39, (1893).
Emery, Zool. Jahrb. Abth. Syst., Vol. 8, p. 266, pl. 8, fig. 10, (1895).
Wheeler, Ants, etc., p. 561, (1919).

Pachycondyla, (Pseudoponera) gilva, Emery, Ann. Soc. Ent. Belg., Vol. 45, p. 46, (1901).

Euponera (Trachymesopus) gilva, Emery, Genera Insect., Ponerinae, p. 86. Wheeler and Gaige, Psyche, Vol. 27, p. 69, (1920).

Euponera (Trachymesopus) gilva subsp. *harnedi,* Smith, Ann. Soc. Ent. Amer., Vol. 22, p. 534, (1929).

It is not necessary to repeat here the description of the worker of *gilva* since a very satisfactory account of this caste has already been given by Wheeler and Gaige ('20). It may be well, however, to mention in passing certain features which were not noted in their description. The greatest width of the head, which occurs approximately at the posterior third, is to the length as 3.7 : 4. The eyes consist of eight or nine poorly defined ommatidia which are partially obscured by overlying pubescence. The penultimate and antepenultimate joints of the funiculus are very slightly longer than broad and not, as has been stated, broader than long. Their true proportions are obscured in dry specimens by the erect hairs which they bear, but become apparent when the specimen is examined in a liquid mount. The ventral surface of the node of the petiole bears a rounded anterior lamella and a somewhat more flattened posterior lobe.

Female.—Length 4.7-5.2 mm.

Head relatively broader than in the worker, its greatest width approximately equal to the length, the sides less evenly convex than in the worker, much narrower in the anterior half than in the posterior, the occipital angles well-marked, the occiput straight or at most very feebly concave. Mandibles large, their external border almost straight, except at the apical third, where it is feebly

convex. Apex of the mandible with a long, stout, sharp tooth, which is longer than any of the other teeth on the masticatory margin, the first three of these large and rather blunt, the innermost three smaller and set very close together. Clypeus with a well-marked, steeply declivious and acutely triangular median lobe, the apex of which lies between the anterior ends of the frontal lobes. Anterior border of the clypeus feebly convex with sinuate lateral terminations. Eyes oval, moderately large, their anterior border separated from the insertion of the mandible by a distance less than the thickness of the antennal scape at its apex. Ocelli of moderate size, equidistant from each other. Frontal lobes flattened, together forming a subcordiform plate which is divided by a longitudinal impression that is continuous with the frontal groove, the latter extending back to the median ocellus. Antennæ twelve-jointed, the funiculus twice as long as the scape. The scape in repose fails to reach the occipital border by a distance one and one-half times its greatest thickness. First funicular joint somewhat longer than the following two together; joints two to seven all broader than long; joint eight as broad as long; joints nine and ten slightly longer than broad; terminal joint slightly longer than the two preceding joints together.

Thorax narrow, its maximum width one-half its length. The dorsum of the thorax in profile feebly convex. Pronotum with a short and very declivious anterior face descending to the neck. Seen from above the humeral angles are much rounded, which with the strongly concave posterior border, gives the pronotum a crescentric appearance. Scutum sub-trapezoidal, one-sixth broader than long, the anterior border strongly convex. Notauli (Mayrian furrows) absent, parapsidal furrows present, extending two-thirds of the distance to the anterior margin of the scutum. Scutellum small, suboval in outline, scarcely half as wide as the greatest width of the thorax. Metanotum very narrow, arcuate in shape. Epinotum seen from above rectangular, the dorsum one-fourth wider than long. In profile the basal face is considerably shorter than the declivious, which it meets at a sharp angle. Petiole very similar to that of the worker, the anterior face steeply sloping, the anterior face virtually perpendicular, the summit

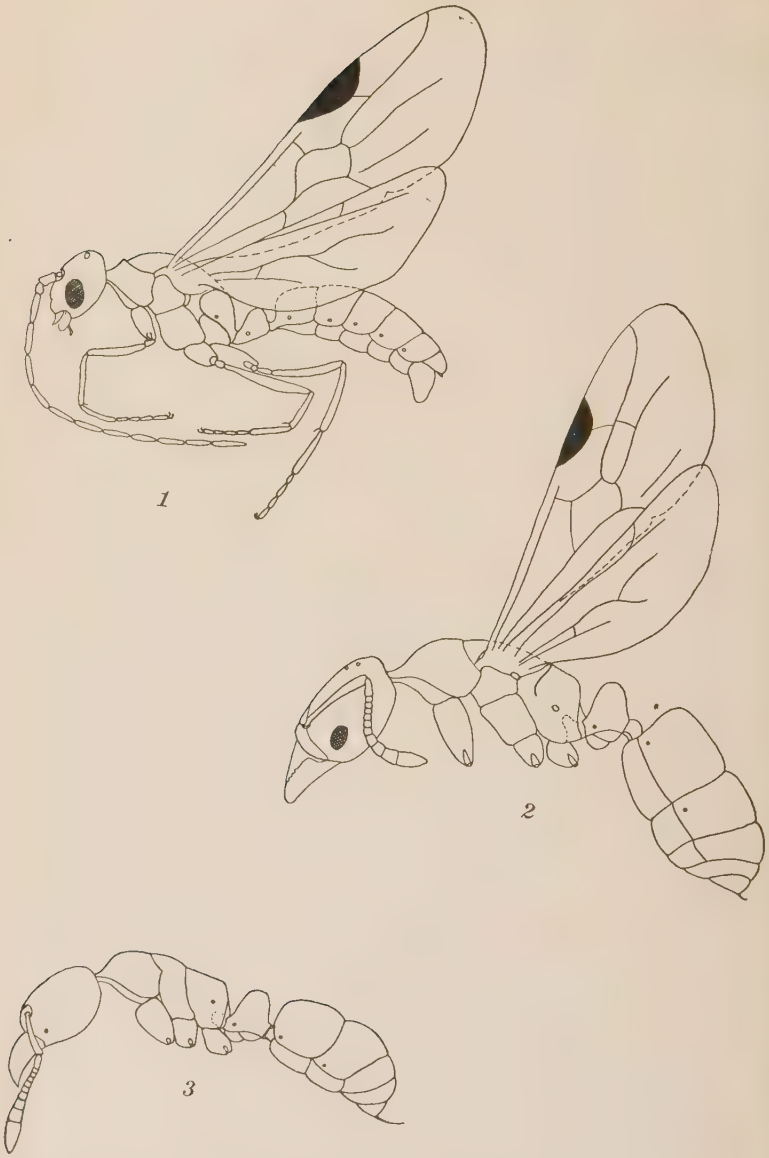

Fig. 1. *Euponera (Trachymesopus) gilva.* 1, male; 2, female; 3, worker.

very thick and obtusely rounded. The ventral surface of the node bears posteriorly a swollen lobe and anteriorly a thin, evenly convex lamella. Seen from above the node is transverse, the apex, which is broader than the more ventral portions, is approximately twice as wide as thick. Gaster elliptical, the constriction between the first and second segments rather feeble.

Color ferrugineous, the head and mandibles somewhat darker, the thorax marked with irregular areas of yellow, particularly on the pronotum and scutum; petiole and abdomen of a somewhat clearer tint, the posterior borders of the gastric segments with broad piceous bands. Antennæ and legs brownish yellow. Cephalic punctures so closely approximated that the head appears to be covered with minute coriaceous rugulae, giving it an opaque texture which shows a dull sheen in certain lights. Thorax more shining, the punctures not so closely approximated, the epinotum somewhat more shining than the rest of the thorax. Petiole and abdomen strongly shining, the punctures about as numerous as those on the epinotum but very small. Mandibles highly glabrous, the punctures very sparse and minute. Head covered with moderately abundant, appressed pubescence, which becomes much longer and coarser on the frontal lobes. Pubescence on the thorax and petiole somewhat finer and sparser. Abdominal pubescence very abundant, longer, coarser and more erect than elsewhere. Erect hairs on the head sparse and short with the exception of one or two very long ones which are inserted at either side of the medium lobe of the clypeus. Those on the thorax longer and more abundant. Erect hairs on the gaster numerous, particularly at the edges of the posterior segments. Tarsi and funicular joints with numerous, short, stout, erect hairs. Wings grizzled, the veins and stigma yellow, the entire wing covered with numerous, fine, short, suberect hairs.

Male.—Length 3.9 mm.

Head subtrapezoidal, much narrowed behind, its greatest width (measured through the eyes) slightly greater than its length, occiput narrow, scarcely wider than the distance

between the lateral ocelli, sides moderately convex. Eyes large, convex, suboval in outline, their margin bounded by a narrow and shallow groove, the posterior border lies at the middle of the side of the head, the anterior border separated from the insertion of the mandible by a distance equal to the thickness of the first funicular joint. Ocelli large and prominent, the two lateral ocelli separated from each other by a distance almost twice as great as that which separates each from the median ocellus. Clypeus subtrapezoidal, the median portion somewhat elevated, the anterior edge feebly sinuate. Mandibles small, rather broad at the base which bears a curious, oval impression, but with a narrow though rounded apex, entirely without teeth, Antennæ filiform, of thirteen joints. First joint cylindrical, about one and one-half times as long as thick; second joint thinner, more rounded, about as broad as long; the remaining joints all much more slender, five times as long as thick.

Thorax seen in profile with a feebly convex dorsum, the pronotum steeply declivious throughout, the small anterior portion forming the neck not well differentiated from the rest; seen from above the pronotum is cresentric in outline and separated from the scutum by a very pronounced suture. Scutum subtrapezoidal, the anterior face evenly convex, its greatest width five-sixths of its length. Notauli (Mayrian furrows) absent, parapsidal furrows extending forward two-thirds of the distance to the anterior margin of the scutum. Scutellum small, rather convex, its dorsum triangular in outline but spreading ventrally to form a quadrate outline. Metanotum thicker and less arcuate than in the female. Epinotum seen from above tapering towards the rear, without sharp definition between the basal and declivious faces. Seen from the side the two faces appear as a continuous curve. Node of the petiole low and thick, the anterior face steeply declivious, the posterior face perpendicular, the summit thick and evenly convex, the ventral surface without lobe or lamella. Gaster very elongate, its greatest width three-eighths of its length, a feeble constriction between the first and second segments.

Color dirty blackish brown, the thorax more or less marked with dirty yellow. The posterior gastric segments

with a narrow band of sordid yellow at the base. Occiput and frontal area piceous. Antennæ and legs dirty yellow. Punctures throughout less numerous than in the female, not sufficiently abundant on the head to produce the opaque appearance characteristic of the female and worker, the head feebly shining. Thorax, except for the epinotum, with the same punctuation as the head. Epinotum, petiole and gaster strongly shining, the punctures very fine and much less abundant. Pubescence on the occiput and front short, fine and appressed; longer, coarser and suberect on the clypeus, thorax and petiole; very long, sparse and suberect on the gaster where it grades into upright hairs at the edges of the segments. Occiput and clypeus with a few long erect hairs. Antennal joints with numerous, short, erect hairs; those of the tarsi, longer, sparser and less erect. Wings grizzled with yellow veins and stigma, the entire wing covered with numerous, short, suberect hairs. In certain lights the wings are iridescent.

THE TYPE FETISH

By J. R. de la Torre-Bueno
White Plains, N. Y.

Professor Embrik Strand writes in Psyche, for September, 1929, an extremely thought-provoking article under the title "Down with the Type Cult"[1], which I translate as in my heading. Whether our personal opinions run with his or not, we must admit he discusses what is becoming an extremely serious matter in entomology. We have types ranging from dipteran ovaries to fragmentary parts of insects, microscopic mounts, and, of course, the whole insect. These are scattered to the four quarters of the globe, in museums and in private collections. In many instances, internal evidence may point to certain specimens or to a series of specimens with which the author worked, but nothing on the specimens themselves shows that these were the ones from which the description is drawn up. Again, we face the condition that a type label may have been carelessly lost or put on a wrong specimen; or even removed or changed of set purpose.

Dr. Strand's idea of doing away with type specimens is not novel. Over twenty years ago, Dr. Verrill, the English dipterist, advocated the destruction of all types and the rejection of all descriptions unintelligible without the type. I have always maintained that paper and ink are far more lasting than specimens; and while we today may have the use of the type material of our contemporaries, it does not follow that our successors will. And even where types are extant, it is difficult to have access to them: Institutions are justly averse to lending types, particularly when these types have far to travel to the borrower. The vicissitudes of a type start when it is taken out of its case and continue

[1]Vol. XXXVI, pp. 228-231.

until it is safely back, perhaps not so entire as when it started, in spite of all the care exercised by both lender and borrower. Who has not at some time received a small box with one or more pins careering madly about in a debris of insect fragments? The policy of institutions is becoming more and more crystallized against the lending of types; and it is necessary now in many instances to inspect types in the parent collection itself, and to have to travel long distances in order to do so.

Another consequence flowing from the type cult is that certain describers content themselves with a one- or two-line, so-called, description; and blandly refer other students to the extant type or types. This saves the describer great labor: *vice-versa* the student.

Of course, these conditions present a full field to the synonym-hounds, who are thus enabled to cast what they please into the discard; or to erect new species on insufficient grounds.

Yet, in view of the extreme parsimony of words of many of the older descriptions and of their authors, what could we do without their types (if extant)?

Figures are sometimes advocated to take the place of types, or to make reference to them unnecessary. But who is to guarantee the accuracy of any figure? If an author makes the drawing, he may not be adept enough to bring out the particular features of the insect which form its basic characteristics (and many of these are impossible to depict in words or in drawing, because they are a part of the habitus or facies of the insect, elusive and difficult to seize upon). Two men may have straight noses, yet each has some fleeting characteristic which differentiates them. Every artist gives these characteristics a personal and probably subjective bent as he protrays them. Uncle Sam as portrayed by an American has an entirely different cast of countenance from the same portrayal by a Japanese, or by a German, or by a Russian, or even by an Englishman. And this is the personal equation of the artist! But when it comes to some other person, no matter how capable, imperceptible (and sometimes obvious) differences creep in. This has happened time and again; and any entomologist may cite numerous instances of these subtle differences,

culled from his own experience. Photography is also suggested as a solution. But photography requires great expertness to attain results. And even here, the very direction of the light may obscure the most important characteristics. The reproduction of the most careful and accurate photograph is also fraught with hazard. Not long since, an entomologist friend of mine had a plate made from a photograph of the venation of an odonate wing. Here is an object all in the same plane, all in lines, possible to photograph exactly, and not depending on light and shade for its accuracy. Yet, the engraver *perfected* the photograph by adding a line where he thought it was needed, thus creating not only a new species, but a new genus as well! And after this come the hazards of proper printing.

All these considerations lead inescapably to the description as the residual *sine qua non*, Dr. Strand's fundamental position as I understand it.

When we arrive at this point, we arrive at the crux of all modern insect taxonomy. The only solution is an adequate description to stand or fall alone, without benefit of types. But what form shall such a description take? Is it to be a taxonomic description, restricted only to selected critical characters? Or is it to be a morphological description taking in each and every structure, internal as well as external? A taxonomic description of *Homo sapiens*, var *entomologus*, might occupy a printed page, but volumes would be required for a complete morphological description. And what are we to do about those who make genitalia the be-all and end-all of specific description?

A modern description, to be acceptable must be in such form as to stand alone independent of a type or of any other description. And by its form it should not only apply to the species described exclusively, but it should also cut all other cognate forms. This eliminates all ambiguity and makes it impossible for one neighbor to be mistaken for another.

When this is done, the type fetish will be automatically abolished, thus attaining the very laudable desire of Dr. Strand.

Et quis custodiet ipsos custodes?

THE WINGS OF THE REMARKABLE ARCHAIC MECOPTERON *NOTIOTHAUMA REEDI* McLACHLAN WITH REMARKS ON THEIR PROTOBLATTOID AFFINITIES

By G. C. Crampton, Ph. D.

Massachusetts Agricultural College, Amherst, Mass.

Through the great generosity of Dr. Edwyn P. Reed, the distinguished Chilean surgeon, I have had the privilege of making an anatomical study of the remarkable archaic Mecopteron *Notiothauma reedi,* McLachlan. In presenting me with the only known specimen of the hitherto undescribed male of *Notiothauma* for dissection and description, Dr. Reed has placed me deeply in his debt, and I would use this opportunity of thanking Dr. Reed for the rare privilege of studying this unique specimen.

The male of *Notiothauma* conforms to the general description of the female in having a castaneous body, but the wings of the male, and those from a specimen which had been damaged by pests (presumably a female, though the sex could not be determined from the remaining fragments) are ochreous, shot through with brown, giving a "brindled" appearance to the incumbent wings.

The male has a remarkable median dorsal process on what appears to be the fourth abdominal tergite (the specimen has not yet been softened for study) and on the next tergite is a pair of rather small lateral tergal processes, while the tergite behind this bears a pair of longer lateral tergal processes, which give a remarkable appearance to the flattened abdomen. The abdomen does not taper like that of a typical Panorpid, and is somewhat suggestive of the abdomen of the Mecopteron Merope, which is rather closely allied to *Notiothauma.*

The genitalia are rather "bulbous" and the basistyles or basal segments of the claspers of the male are rather short and stout; and the dististyles or distal segments of the claspers, unlike those of *Merope* (which has long slender dististyles) are shorter and stouter, and are somewhat furcate, with the exterior terminal branch curving outward (laterad) to some extent, apparently for the purpose of lying on either side of the median dorsal process (described above) when the genitalia are held forward in repose.

I would designate this hitherto undescribed male as the allotype of *Notiothauma reedi,* McLachlan, and a detailed description of it will be presented in a later paper dealing with the morphology of this remarkable Mecopteron, which is the only scorpionfly with flat incumbent wings (see Plate 2).

There is no fundamental difference between the wings of the male and those of the damaged specimen (presumably a female), so that the accompanying description of the wings of the supposed female will serve to illustrate the later description of the venation of the male, in describing the alar ossicles and other features of the basal region of the wing, in discussing the morphology of the male insect.

The measurements of the wings are as follows: Length of fore wing, 23.5 mm.; greatest width of fore wing, 10 mm.; length of hind wing, 22 mm.; greatest width of hind wing, 9 mm. The fore wings are more deeply pigmented and are ochreous, while the hind wings are more hyaline, and have a yellow tinge. The fore wings are like delicate tegmina, apparently derived from Protoblattoid (Protoblattid-like) or Protorthopteroid (Protorthoptera-like) prototypes, but the hind wings have lost the anal fan characteristic of the Protoblattids, etc., as likewise have the Isoptera (except Mastotermes), for that matter, which are the direct descendants of Protoblattoid forbears. The fore wings are somewhat broader in the distal half of the wing, and are broadly rounded apically, resembling in these respects the fore wings of the Protoblattids *Asyncritus, Adiphlebia,* etc., figured by Handlirsch, 1925 (Schroeder's "Handbuch," Band 3), or the Protorthopteroid insect *Metropator,* figured by Handlirsch, 1909 (Die Fossile Insekten). These are Protoblattoid features pointing to a

Protoblattoid ancestry for the Mecoptera, instead of indicating an ancestry for the Mecoptera in forms like the Megasecoptera or even the Palæodictyoptera.

The Megasecoptera and Palæodictyoptera are Archipterygota, or insects incapable of folding the wings along the abdomen in repose, while the Protoblattids and Protorthoptera are Neopterygota, or insects capable of laying the wings along the abdomen in repose, and the Protoblattids and Blattids typically hold the wings in the recumbent position in repose (i. e., the wings laid flat, one on top of the other, on the top of the abdomen) and it is a very significant fact that Notiothauma holds its wings in the incumbent position in repose, so that this archaic Mecopteron must have been descended from Neopterygotan ancestors rather than from Archipterygotan ancestors such as the Megasecoptera, etc., regarded by Handlirsch and Tillyard as the ancestors of the Mecoptera. (See Plate 3)

The basal arch (*ba* of Figs. 1 and 7) of the first anal vein, forming a typical "basoplica," together with the fold-like depression, like that described by Crampton, 1927 (Psyche, 34, p. 59) and 1928 (Bull. Brooklyn Ent. Soc., 23, p. 113) in the Blattids, Isoptera, Orthoptera, Cicadas, Trichoptera, etc., which have developed these structures in connection with laying the wings along the abdomen in repose, likewise indicates a Neopterygotan ancestry for the Mecoptera.

The formation of cellules in the wings of the Protoblattids *Asyncritus, Adiphlebia,* etc., suggests the beginnings of a tendency to form cellules in the fore wings—a tendency which has been carried to an extreme in *Notiothauma.* It should be noted that it is not necessary for all of the Protoblattids or for all of the Mecoptera to exhibit this tendency in order to derive the Mecoptera from a Protoblattoid ancestory, since, according to the adumbration theory, some members of an ancestral group may exhibit tendencies which later reappear in some members of a derived group without these features being exhibited by all, or most, of the members of either group, as has been discussed elsewhere. It is therefore illogical to demand that all of the Protoblattoids shall exhibit a tendency toward the formation of numerous cellules, in order to derive such a

Mecopteron as *Notiothauma* (with its many cellules) from Protoblattoid ancestors.

In both the fore and hind wings of *Notiothauma*, there is a postero-basal lobe, or jugalula, labelled *a* in Figs. 1 and 2, which is called the alula in Coleoptera, etc., but the term alula was long ago used by Osten-Sacken, 1896 (Berlin Ent. Zeit., 41, p. 285) to designate an entirely different structure, namely the anal lobe of the Dipterous wing (i. e., the lobe distal to the calypteres) ; and it is preferable to refer to the jugalular lobe as the jugalula, since it is homologous with the jugalula of the roach. Esben-Petersen, 1921 (Mecoptera in Coll. Zool. Selys Longchamps) calls these jugalulæ the "clavi" in *Notiothauma*, but the clavus is an entirely different region, homologous with the anal region presently to be described, and there is no excuse for applying the term clavus to any structure other than the region homologous with the clavus of the Hemiptera. The jugalula *a* is bordered by a fringe of hairs labelled *af* in Figs. 1 and 2, and when the jugalula *a* of the fore wing (Fig. 1) is folded forward under the fore wing, it engages the bristles labelled *bsc* in Fig. 2 of the hind wing, thus serving as a primitive type of jugum. In my specimens, the jugalula was folded forward, and it was very difficult to make out its structure in the mounted wings.

The basicostal bristles *bcs* of Figs. 1 and 2, are borne on a thickened, antero-basal, marginal structure in both wings; and these bristles in the hind wing are apparently the forerunners of the frenulum of higher insects, although they can hardly be called a frenulum on the fore wing. These bristles are unusually stout and long, and belong to the type of bristle which may be called dinotrichia, or powerful bristles, such as those occurring on the veins, etc., at the base of the fore wings (Fig. 7) or on the thorax, etc., Macrotrichia occur on the costal margin of the wings in the neighborhood of the humeral veinlet *h* of Figs. 1 and 2, and gradually become smaller toward the middle of the wing, (they are not drawn in this region of the wing in Figs. 1 and 2). The "dinotrichia" occurring on some of the veins in the basal region of the fore wing are shown in Fig. 7, and the sockets or pits, which are left when such bristles are broken off, are shown in the figure. Macro-

trichia occur on the ventral surface of the basicostal structure labelled *bc* in Fig. 4, and on the ventral surface of the humeral veinlet *h* of Fig. 4; and a row of macrotrichia occurs on the ventral surface of the subcostal vein shown in Fig. 4. This row of macrotrichia may aid in holding the wings in place in repose.

Forbes, 1924 (Ent. News, 35, p. 232) in describing the nygmata of Holometabolous insects, states that in "*Merope* and apparently *Notiothauma* nygmata are absent," but I find in the basal costal cell, for example, what appears to be the homologue of a nygma, similarly located to that of *Panorpodes* (see *n* of Fig. 7), and nygmata are thus apparently present in the fore wings of *Notiothauma*, although I have not examined Merope to determine if they are present in this insect also.

The venation of the hind wings is quite easily homologized, but the tangle of cellules in the distal portion of the fore wings makes it extremely difficult to trace the course of the veins in this region of the fore wings, so that the course of the distal portions of such veins as the second, third and fourth branches of Media is merely suggested, although the basal portions of these veins are quite easily homologized.

The fore wing has preserved a suggestion of a humeral lobe in the curved contour of the basal portion of the wing just anterior to the label *h* in Fig. 1 (which is a Protoblattoid or Protorthopteroid feature) and the costal vein has become interrupted just basad of the humeral veinlet *h* of Fig. 1. The detached basal portion of the vein becomes broadened (to accommodate the large bristles *bsc*) and forms a structure homologous with the sclerite called the basicosta in the roach, Mantids, Trichoptera, Cicadas, etc. (Psyche, 34, p. 59, and Bull. Brooklyn Ent. Soc., 23, p. 113). The occurrence of such a basicostal sclerite in *Notiothauma* indicates that its fore wing was derived from a Blattoid or Protoblattoid prototype rather than from a wing of the type occurring in the Archipterygotan insects (which have no such sclerite). I find a trace of the basicostal sclerite even in the hind wing of such a highly specialized insect as the monarch butterfly *Danaus archippus* ("Anosia plexippus") in which the costal vein fades out

and the humeral veinlet is retained to support the weakened humeral lobe. In the hind wing of *Malacosoma* and other Lasiocampids there are two veinlets called the humeral cross veins by Comstock, 1924 (An Introduction to Entomology) but I think it preferable to restrict the term humeral veinlet to the first veinlet *h* of Figs. 1 and 7, and to refer to the one distad of it as the posthumeral veinlet (i. e., *ph.* of Fig. 7). These structures are referred to as veinlets rather than as cross-veins, since they are homologous with the veinlets of the Neuroptera, etc. The humeral veinlet *h* of Figs. 1 and 7, is much stouter than the other veinlets; and the weaker posthumeral veinlet *ph* is more pronouncedly curved.

The veinlets in the broad costal area of the fore wing have branched or are connected by cross veins in an irregular fashion causing a distortion of the veinlets and producing numerous cellules, which are irregularly pentagonal or hexagonal in the basal region and are more elongated and subquadrate in the distal region of the costal area. The broad costal area apparently represents a condition inherited from Protoblattoid ancestors resembling *Asyncritus* in some respects, and the curve in the costal margin of the fore wing may also represent the retention of a tendency more markedly developed in the Protoblattoid insects, instead of these features representing a type of specialization peculiar to *Notiothauma.*

As is true of Mecoptera in general, the subcostal vein *Sc* of the fore wing (Figs. 1 and 7) is a concave vein, and a minus sign (-) has been placed above it in Figs. 1 and 7, to indicate this fact. The base of *Sc* dips below the base of the radius R, as is indicated in Fig. 7. After paralleling R for some distance, *Sc* ends at the pterostigma *pst* of Fig. 1, although some of the branches of *Sc* appear to penetrate the pterostigma for a short distance. The wide separation of *Sc* from the costal margin, and its paralleling R for such a considerable distance are Protoblattoid features apparently inherited from a Protoblattoid ancestry.

The radial vein R is higher than the concave vein Sc, and appears to have much the same character as that of R_1 which is a convex vein, so that R may be regarded as a convex vein, although its sector R_s seems to be a concave

vein. R fuses with M basally, and is contiguous with M until it forks—or rather, the space between R and M is sclerotized giving the appearance of a union between the two veins, although the veins themselves are not as closely contiguous as this pigmentation or sclerotization of the intervening membrane would suggest (See Fig. 7). R_s is given off in the basal fifth of the wing, and is richly branched, being somewhat like the radial sector of the Protoblattid *Stenoneura* in this respect, though it is of course much more like the venation of such primitive fossil Mecoptera as *"Protomerope,"* or the primitive fossil Neuropteron *Permorapisma* (particularly the latter) than it is like the Protoblattids, since the Mecoptera and Neuroptera are naturally more closely related to *Notiothauma* than the Protoblattids are. The convex vein R_1 is apparently unbranched and extends distally below the pterostigma *pst* almost to the margin of the wing, although a short backward extension of the pterostigma in this region intervenes between the margin of the wing and the tip of R_1. The concave radial sector R_s is given off in the basal fifth of the wing, and is richly branched with numerous cellules between the distal portions of its branches, and the cellules tend to become elongated and more quadrilateral than the cellules of the costal or cubital regions. It is quite easy to trace the branching of the radial sector, and the branching of its forks into R_2 and R_3 or into R_4 and R_5, in the basal portion of the wing, but the tracing of the courses of these branches in the distal portion of the wing is not as easy a matter as it is in such forms as *Merope* or even *Permorapisma,* due to the fact that the course of these branches is obscured by the tangle of cellules in *Notiothauma,* and on this account the interpretation of the branches of radius in the figure of the fore wing is purely tentative, although in the hind wing of *Notiothauma* the course of these branches can be followed with ease.

M seems to be a concave vein, although it fuses with *R* basally and is contiguous with *R* in the basal region of the wing. The branches of *M* are also concave veins, so that it should be an easy matter to distinguish the course of these veins from that of Cu_1 which is a convex vein, but

the course of the median veins is so extremely aberrant, that I am the least confident of my interpretations in this region of the fore wing, although of course it is an easy matter to interpret the median veins of the hind wing. I have figured the median veins of the wings of *Notiothauma* from all available sources, using the original photograph (which is much clearer than the published figure) from which the illustration of Dr. C. E. Porter's note on *Notiothauma* was made (Revista Chileana Hist. Nat., 1929, XXXIII, p. 288),—Dr. Porter having very kindly sent me the original photograph—and I have also used Esben-Petersen's figure of the wings of *Notiothauma*, but even with these figures to aid me, in addition to examining the wings of two specimens of *Notiothauma*, I am not very sure of the course of the branches of M in the fore wing! In his review of Imms' book, Tillyard, 1926 (N. Z. Jour. of Science and Technology, 8, p. 127) states that the "thyridium is a hyaline area on M just before it forks" in Trichopterous wings, and there is a clear spot at the forking of M in Nannochorista, Sisyra, etc. Since there is a hyaline area (resembling the so-called bullæ) labelled *b* in Figs 1, 3, 4, 5 and 6 at the base of what Esben-Petersen (1. c.) considers as the first fork of *M* in the fore wing of *Notiothauma*, I feel almost certain that the forking of M is at the point labelled *b* in these figures. This interpretation, however, would leave a whole vein unaccounted for (can this be M_3?) but lying between the concave anterior branch of M and the convex anterior branch of Cu (i. e., Cu_1, whose course is indicated by a + sign in Fig 1) in these figures. Unlike the typically short M_3 of most insects (although M_3 is longer in some Psychopsidæ), the vein in question is of considerable extent, and joins the rest of the branches of M instead of extending across to Cu_1 as the vein M_3 usually does, and as is done by the vein labelled M_3 in Fig. 1, etc. I am therefore inclined, purely provisionally, to interpret as the first forking of M, the fork which is located just distad of the dotted line running up from the label M in Fig. 1. This fork occurs in all of the wings, and figures of wings, which I have seen; so it can hardly be an added cross vein that has taken on the appearance of a fork in one specimen: furthermore, it is continued

in the vein labelled M_3 in Fig. 1—although it may possibly continue on down and fuse with Cu_1 instead, but the latter view is not very probable (although it should be considered as a possibility), because it would leave the vein labelled M_3 unaccounted for. I am therefore inclined purely provisionally to interpret the fork of M just distad of the dotted line running up from the label M in Fig. 1 as the forking of M into M_{1+2} and M_{3+4} as is indicated by the labelling. The fork at the hyaline spot labelled *b* in Figs. 1, 3, 4, 5 and 6, would then be the forking of M_{1+2} into M_1 and M_2. Where the forking of M_{3+4} into M_3 and M_4 is, I do not know, although I am inclined to think that it may be just basad of the dotted line running up from the label M_3 in Fig. 1. If this be correct, M_3 would be the vein so labelled in the Figure, while M_4 would be the short vein extending to and fusing with Cu_1 in Fig. 1. On the other hand, this short vein may be merely a cross vein between vein M_{3+4} and Cu_1, in which case the vein labelled M_3 in Fig. 1 would in reality be vein M_{3+4}. I have provisionally followed the former view and have labelled the median veins as though M_4 had fused with Cu_1 in Fig. 1. There is such a disconcerting tangle of cellules (which are more elongate and quadrangular in the medial region than in the cubital region) in the medial region, however, that I would not insist on the interpretation of the courses of the branches of *M* indicated by the labelling, and the final interpretation of these veins must await the study of the pupal tracheation, or the comparison with some less complicated venation in the fore wing of some as yet unknown Mecopteron. *Merope* and *"Protomerope,"* however (both of which are related to *Notiothauma*) are primitive Mecoptera with a less complicated venation which shows no indication of a fusion of M_4 with Cu_1, and this fact makes me suspect that the vein labelled M_3 in Fig. 1 is in reality vein M_{3+4} and the forking of this vein into M_3 and M_1 occurs further out toward the distal half of the wing, and the labels should therefore be shifted accordingly in Fig. 1. The development of the medial field is much greater in *Notiothauma* than in most Protoblattids, but some of the Protoblattids, such as *Eucaenus*, have a four branched media such as the ancestors of the Mecoptera must have had.

The cubital field of *Notiothauma* is filled with broader irregular pentagonal or hexagonal cellules and the cubital field is remarkably like that of such Protoblattids as *Asyncrytus*. The extremely short basal portion of Cu (i. e., before it forks) is another feature strongly suggestive of these Protoblattids, and is an added feature pointing to a Protoblattoid ancestry for *Notiothauma* (and hence for the Holometabola in general). As was mentioned above, Cu_1 is a convex vein (as is indicated by a + sign in Fig. 1) and Cu_2 is a concave vein (indicated by a — sign in Fig. 1), and this seems to be characteristic of all Mecoptera. As occurs in the wings of some fossil, but no other Mecoptera, Cu_1 branches into Cu_1 a and Cu_1 b judging from the condition exhibited by the hind wing, but I am not certain where this occurs in the fore wing unless it be at or just beyond the point where the dotted line running up from the label M_1 in Fig. 1 crosses Cu_1. As is also true of the Mecopteron *Panorpodes*, a nygma or wing spot, occurs in the basal cubital cell, as is shown in Fig. 7, where the nygma is labelled *n*. Just behind Cu is the preclaval rima or crack-like line demarking the anterior limits of the claval or anal area. This crack frequently interrupts the basal portion of Cu, and may have been formed in connection with the developing ability to lay the wings back in the incumbent position.

The anal or claval area (i. e., the clavus of Hemiptera) extends from the above-mentioned claval rima to the jugalula labelled *a* in Fig. 1, and contains the three anal veins which are convex veins in Mecoptera in general. The first anal, labelled 1. A. in Fig. 1, has a well developed basal arch labelled *ba* which occurs as a basal ridge, with an accompanying pocket or fold developed in connection with the ability to lay the wings back along the abdomen in repose. The weakening of the costal margin and the consequent detachment of the basicostal sclerite or protuberance *bc* of Fig. 1, is probably also developed in connection with the folding of the wings along the abdomen in repose, so that all of these features are of importance from the phylogenetic standpoint, and it is surprising that no one has referred to such features in the wings of insects. I have found them in the Blattids, Isoptera, Cicadas,

Gryllacridæ, Panorpids, etc. (Psyche, 34, p. 59 and Bull. Brooklyn Ent. Soc., 23, p. 113), and when such an important form as the fossil *Metropator* is figured with a basal arch in the first anal vein by Tillyard, 1926 (Amer. Jour. of Science, 11, p. 161) I think that this (together with the outline, venation, etc. of the wing) indicates that *Metropator* is more closely related to the Protorthopteroids than to the Palaeodictyoptera, although Handlirsch places *Metropator* in his order Palaeodictyoptera, and not in the order Protorthoptera as Tillyard states. *Eubleptus* (order Eubleptoptera) may be nearer the Palaeodictyoptera, but *Metropator* (Metropatoroptera) evidently represents a type worthy of ordinal rank, closely related to the Protorthoptera, and with a venation approaching that of some Mecoptera with reduced venation, through convergence. *Metropator* lacks the costal veinlets, the forked Cu_1 and other features which were undoubtedly present in the ancestral Mecoptera, and I think that Tillyard, 1926, is mistaken in considering this Protorthopteroid insect as an ancestral Mecopteron.

The resemblance of the wing of *Metropator* to that of a Mecopteron with reduced venation, is apparently due to convergence, or possibly to adumbration and the relationship of *Metropator* to the Mecoptera would be by way of a common Protorthopteroid or Protoblattoid ancestor, and would not be the direct relationship of ancestral and derived types.

As was mentioned above, the first anal has a well developed basal arch. The second anal is not so pronouncedly arched, and joins the third anal basally. The third anal has an almost straight trunk (anotruncus) which gives off four branches unilaterally—though some of these may be branches of the second anal vein. The cellules filling the anal or claval area make it very difficult to determine the course of the anals and their branches, and the interpretation here given is truly provisional. The trunk of the third anal demarks the claval or anal area from the jugalula *a* of Fig. 1 in many insects, and is a fairly serviceable landmark in *Notiothauma*.

Esben-Petersen refers to the jugalula *a* of Fig. 1, as the "clavus," but this lobe is not the homologue of the clavus

of the Hemiptera, etc., and should not be designated as such. This lobe is homologous with the so-called alula of Coleoptera, etc., but the term alula was applied to the anal lobe of the Dipterous wing by Osten-Sacken, 1896, as was mentioned above, and since the jugum is formed in this region, it is preferable to refer to it as the jugalula, as in the case of the homologous structure in the roach and other insects (Isoptera, etc., described in Bull. Brooklyn Ent. Soc., 23, p. 113 and Psyche, 34, p. 59). The veins in the lobe labelled *a* in Fig. 1 may be called the axillary or postanal veins. They serve to strengthen the lobe when it is used as a jugum, as is the case in the fore wing of *Notiothauma*. They are apparently absent in the hind wing, since the lobe is not used as a jugum in this wing. The elongated sclerite just below the label *ba* in the lobe of the fore wing (Fig. 1) is probably the homologue of the alar ossicle called the basanale in the roach, etc. (paper cited above). The jugalular lobe *a* of Figs. 1 and 2 is bordered by the axillary cord or ligamentum, which bears a fringe of hairs labelled *af* in Figs. 1 and 2.

Since the venation of the hind wing is comparatively simple, it will not be necessary to discuss each of the veins in detail, and the labelling of the wing will be sufficient to indicate the homologies of the veins. There are a few points, however, which merit separate consideration in comparing the two wings.

The hind wing is somewhat shorter and narrower than the fore wing in actual millimeters, but in proportion to its length, the hind wing is a little broader (proportionately) than the fore wing, and is a little narrower at its base than the fore wing is. Its jugalular lobe *a* (Fig. 2) is likewise somewhat weaker than the corresponding lobe of the fore wing (*a* of Fig. 1).

The hind wing has no such pronounced curve in the costal margin beyond the humeral veinlet *h* (Fig. 2) as occurs in the fore wing (Fig. 1), and the cellules in the costal region of the hind wing are less numerous than in this region of the fore wing. The costal veinlets of the hind wing are more "normal" or regular; and the costal space is not so broad in the hind wing as it is in the fore wing.

The cross veins of the hind wing, like those of the fore

wing, are frequently broken by "pellucidæ" (maculæ pellucidæ) or "bullæ," which are clear spots. Their true function is not definitely known. Only a few of these are indicated in the figures.

The cellules of the hind wing are not as irregular as those of the fore wing, and the venation of the hind wing is more "normal" than that of the fore wing, particularly in the medial field. M_5 is not labelled in Fig. 2, but it can be identified by the dotted line running up from M_{3+4}, which crosses M_5. Since M_4 is not fused with Cu_1 in the hind wing, I am inclined to think that it is not fused with Cu_1 in the fore wing either, so that the vein labelled M_3 in the fore wing is probably M_{3+4}.

The stem of Cu is extremely short in the hind wing (Fig. 2) and its fork looks more like a cross vein than a fork. Cu_1 is not united with M, and it forks into Cu_1 a and Cu_1 b, which is a very primitive feature not retained in other living Mecoptera, and the character of Cu, with its short stem, is suggestive of a Protoblattoid origin.

The first anal vein of the hind wing is not markedly curved at its base, and the second anal vein parallels it rather closely. The trunk of the third anal gives off three branches anteriorly (unilaterally) which leads me to think that the third anal of the fore wing branches in the same fashion. The fact that the anals exhibit no tendency to loop up as they do in the fore wings of certain Trichoptera, etc., shows that *Notiothauma* is a rather primitive Holometabolan, and its venation and wing characters indicate that it is one of the most primitive members of the order Mecoptera.

In referring to the "Protoblattoid" or "Protorthopteroid" ancestors of higher insects, it should be borne in mind that the Protoblattids and Protorthoptera are fundamentally alike, and the division into these two groups is one of convenience rather than a division into groups of ordinal rank, since the Protoblattids and Protorthoptera intergrade so markedly that it is doubtful that they represent groups of more than subordinal rank. Since the two groups thus intergrade, the terms "Protoblattoid" and "Protorthopteroid" are practically interchangeable because the Protoblattids are in reality "Protorthopteroid" or Protorthop-

tera-like, and the Protorthoptera are in reality "Protoblattoid" or Protoblattid-like, and it would be correct to state that the ancestors of the Mecoptera and other Holometabola were either Protorthopteroid or Protoblattoid; but since the Protoblattids are a little nearer the common stem forms from which the others were derived, it is somewhat more accurate to describe the ancestors of the Holometabola, etc., as "Protoblattoid." A study of the wings of such a primitive Mecopteron as *Notiothauma* very clearly indicates that the ancestors of the Mecoptera had (1) delicate tegmina, (2) wings which were broader in the distal half of the wing and were (3) broadly rounded apically. The wings were (4) incumbent in repose, and, to facilitate laying the wings back in repose, had developed (5) a break in the basal costal region, resulting in the formation of (6) a basicostal sclerite demarked from the rest of the costal vein, (7) a basal arch of the first anal vein with an accompanying (8) basal pocket or fold, and (9) a preclaval rima or crack which traverses the base of the cubital vein and aids in permitting the wing to be laid back in repose. (10) The costal area was very wide, and (11) cellules tended to develop in it. (12) The stem of Cu^1 was very short and (13) irregular cellules filled the cubital area. (14) The fore wings bore a jugalular lobe. Most of these features occur in the Protoblattids, and in many of their living representatives, the Blattids (indeed, some entomologists do not recognize the Protoblattids as an order distinct from the Blattids); but these features are not characteristic of the Megasecoptera and other forms which have been proposed as the types ancestral to the Mecoptera. I would therefore maintain that the ancestors of the Mecoptera were Protoblattoid, and from such ancestors arose all of the lower Holometabola—and in fact of the Hemipteroid insects as well.

The types intermediate between the Protoblattoids and the ancestral Mecoptera are as yet unknown, but the immediate ancestors of the Mecoptera must have been extremely like those of the fossil Neuropteron *Permorapisma*, although the wings of *Permorapisma* itself, are not rounded

[1] Cu_1 was probably forked in the ancestral Mecoptera.

apically (see figure by Tillyard, 1926, Proc. Linn. Soc. N. S. W., 51, p. 278). In the American Journal of Science, 11, p. 133, Tillyard, 1926, proposes that the fossil Mecopteron, which he calls *"Protomerope,"* is ancestral to *Merope* and probably also to *Notiothauma,* but the shape of the wing of *"Protomerope"* is different from that of *Notiothauma,* the anals are not as primitive as those of *Notiothauma,* the first branch of Cu (i. e., Cu_1) is not forked as in *Notiothauma* (which is a very primitive feature in *Notiothauma*); and many other features prevent our deriving Notiothauma from *"Protomerope,"* which is more specialized in these respects than *Notiothauma* is. Under these conditions all that can be said of the hypothetical "Protonotiothaumidæ" ancestral to the Notiothaumidæ and Meropidæ, is that they were Protomecoptera, in which suborder the superfamily Meropoidea, including the Meropidæ and Notiothaumidæ, belongs.

The family Choristidæ (superfamily Choristoidea), which occupies a position at the base of the suborder Eumecoptera, may be descended from the fossil Permopanorpidæ, but the Choristidæ themselves, are so primitive in many respects, that they probably arose from forms more primitive than the Permopanorpidæ, and of a type almost as primitive as the ancestors of the Notiothaumidæ.

The Nannochoristidæ (superfamily Nannochoristoidea) possibly descended from the fossil Mesochoristidæ. There are several features, however, which suggest that the Nannochoristidæ and Panorpodidæ (*Panorpodes*) may have descended from ancestors resembling those of the fossil Mesopanorpidæ, and the shortened head in *Nannochorista* and *Panorpodes* may be a feature of some phylogenetic significance.

The Panorpidæ (superfamily Panorpoidea) were probably descended from the fossil Orthophlebiidæ. The Boreidæ (superfamily Boreoidea) were apparently descended from ancestors like the Panorpidæ. The Boreidæ, however, have an entirely different type of terminal abdominal structures (in both males and females) from those of the Panorpidæ, and the Boreidæ have become so extremely specialized that they might be placed in a distinct suborder, the Neomecoptera, distinct from the Eumecoptera, mentioned above.

The Bittacidæ (superfamily Bittacoidea) are quite different from the rest of the Mecoptera in the character of the terminal abdominal structures of the male and female, and their slender bodies are modified along lines leading away from the typical scorpionfly trends. I, therefore, have no hesitancy in placing them in a distinct suborder, the Metamecoptera. The origin of these insects is obscure, although there is some evidence that they might have descended from the same ancestors from which the fossil Neorthophlebiidæ, were derived. It is more probable, however, that the Bittacidæ were derived from ancestors resembling those of the Panorpidæ. In the character of the male genitalia, the Choristidæ suggest the origin of the peculiar type occurring in the Bittacasidæ, and this might be taken to indicate a common ancestry for the Choristidæ and Bittacasidæ. The terminal structures of the female, however, would not bear this out, and until more is known of the comparative anatomy of the Mecoptera, it will be impossible to determine what family is the most closely related to the Bittacidæ, which occupy a rather isolated position in the order Mecoptera.

The terminal abdominal structure of the female Mecoptera have been figured in the December, 1928, issue of the Journal of the N. Y. Entomological Society, and the features referred to above are shown in this paper. The genitalia of the males of the Mecoptera referred to above are shown in a paper published in the Trans. of the American Ent. Society, 1923, 48, p. 207. The terminal structures of related Mecoptera will be discussed in the paper dealing with the male of *Notiothauma,* in which the anatomical features of the allotype will be shown in detail.

Abbreviations

A. Anal veins.
a. Jugalula or "alula," containing the axillary veins.
af. Alafimbrium or alular fringe.
b. Bullae or "pellucidae."
ba. Basarcus, or basal arch of the first anal vein.
bc. Basicosta.
bcs. Basicostal bristle.s

C. Costal vein.
cs. Costal rima or suture.
Cu. Cubital veins.
ds. Dinotrichia or powerful bristles.
h. Humeral veinlet.
M. Medial veins.
n. Nygma.
ph. Posthumeral veinlet.
pst. Pterostigma.
R. Radial veins.
s. Sockets of bristles.
Sc. Subcostal vein.

Explanation of Plates 2, 3, 4 and 5.

Fig. 1. Fore wing of Notiothauma (female).
Fig. 2. Hind wing of same.
Fig. 3. Veins of fore wing, from photograph by Dr. Porter.
Fig. 4. Ventral view of veins of fore wing.
Fig. 5. Veins of fore wing of male allotype.
Fig. 6. Veins of fore wing from figure by Esben-Petersen.
Fig. 7. Enlarged view of basal portion of fore wing of female.

Plate 2 shows a lateral and a dorsal view of the allotype, male, of *Notiothauma reedi,* McL., from photographs made by Professor Davis, of the Department of Botany, M. A. C. In these photographs the Blattoid appearance of Notiothauma is well shown. Note particularly the flat incumbent wings, which are unlike those of any other living Mecopteron, in this respect. The figures of Notiothauma, with wings outstretched, do not give a correct idea of the remarkable appearance of this peculiar insect, as may be seen by comparing them with the photographs here given. The photographs are larger than "life size," in order to show the intricate venation.

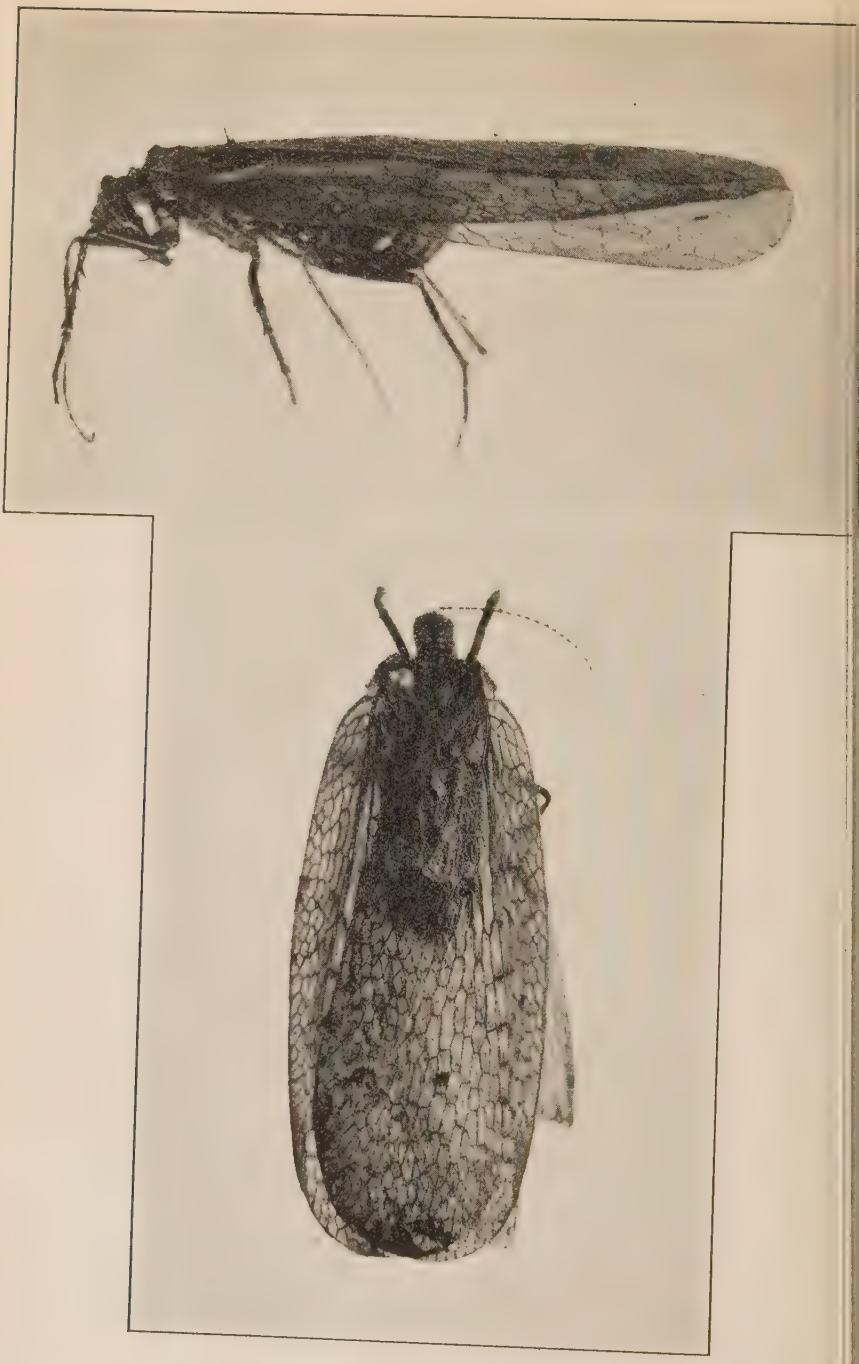

PLATE 2
Crampton—Notiothauma

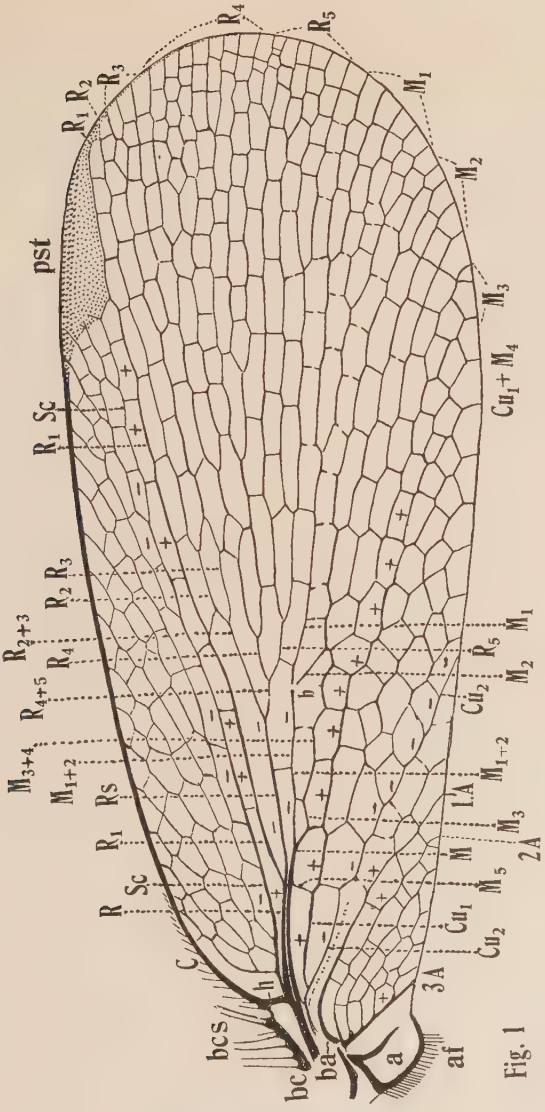

PLATE 3
Crampton –Notiothauma

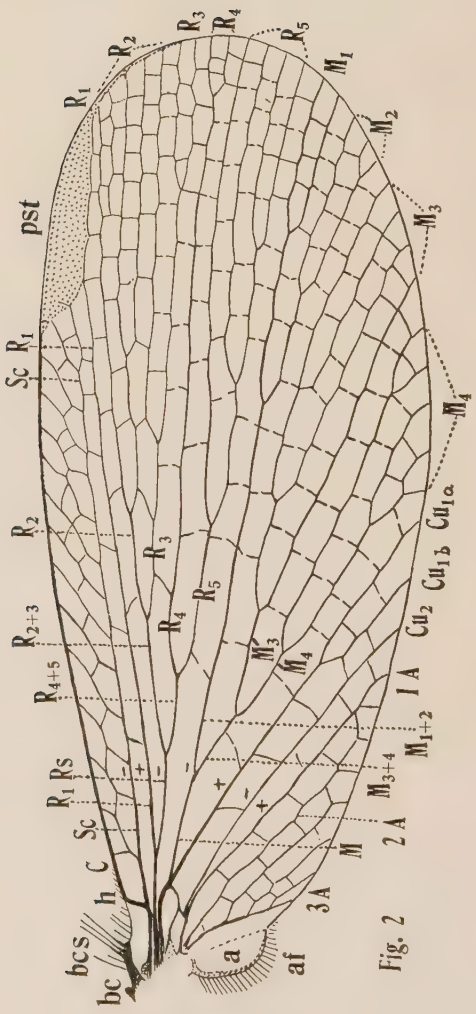

Fig. 2

PLATE 4

Crampton—Notiothauma

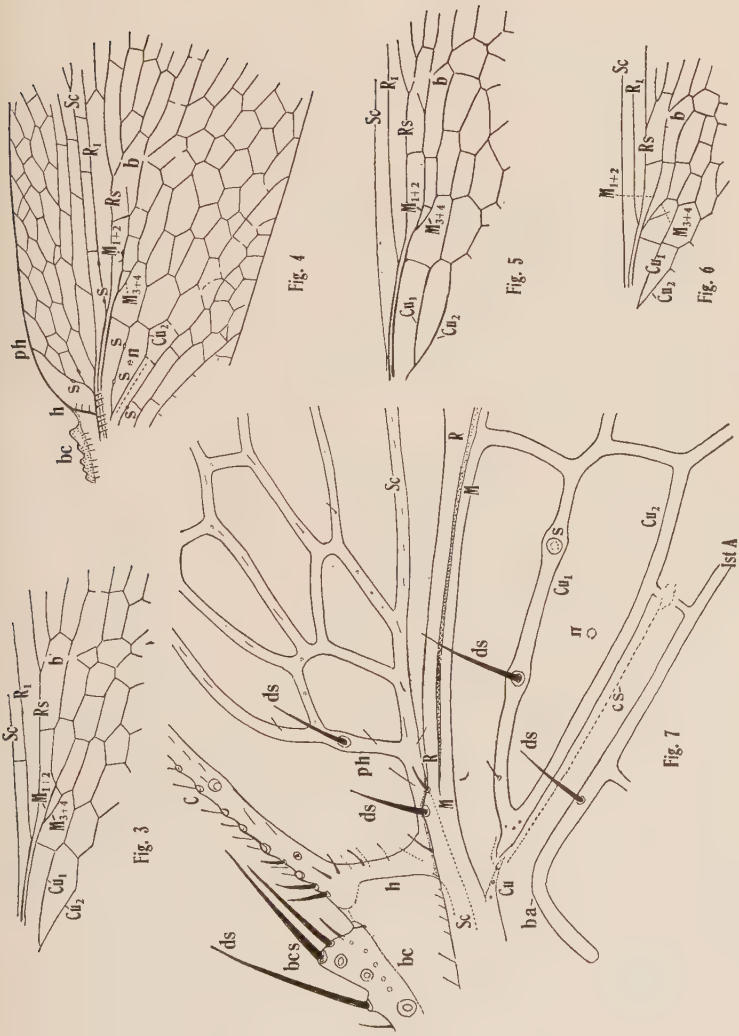

PLATE 5
Crampton—Notiothauma

A NEW NEBRIA FROM MOUNT RAINIER

By P. J. Darlington, Jr.

An examination of the types of *Nebria kincaidi* Schwarz and *N. columbiana* Casey, which the authorities of the United States National Museum kindly permitted me to make recently, proves that the two species are absolutely identical. Schwarz's name has priority. This leaves the insect which has sometimes gone in collections as *Nebria columbiana* Casey without a name, so I propose that it be called

Nebria vandykei sp. nov.

Moderately stout, legs and antennæ slender. Color nearly uniform piceous or reddish piceous, but with the antennæ and parts of the under surface more or less rufescent; the head with two poorly defined reddish spots between the eyes; the elytra with weak purplish reflections. Head about five-sevenths as wide as the prothorax, eyes only slightly more prominent than the sides of the head behind them, antennæ more than one-half as long as the entire body. Prothorax about five-eighths as long as broad, strongly cordate, with the sides arcuate in anterior two-thirds and reflexed before the acute posterior angles; prothoracic base and apex moderately emarginate, base about five-eighths as wide as widest part; pronotum only slightly convex, median longitudinal line narrow and well impressed, basal and apical transverse impressions variable but usually well impressed, lateral margins rather narrowly reflexed. Elytra about three and two-thirds times as long as the prothorax and one-third to two-fifths wider, elliptical, with the widest point behind the middle; humeri narrow, completely rounded into the sides as in *Nebria ovipennis;* striæ deep, very finely and rather sparsely punctured; intervals posteriorly with a few inconspicuous inter-

ruptions. Inner wings only about one-third as long as elytra.

Length 10-13 mm. Width 4-5+ mm.

Holotype ♂ and allotype ♀ in the writer's collection from MOUNT RAINIER, WASHINGTON, near Paradise Valley, just below snow line at about 6000 feet elevation, July 18 and 13, 1927. A good series of paratypes from the same locality, July 13 to 20. All specimens taken by the writer. There is some variation in the precise form of the basal angles of the prothorax and in the punctuation of the elytral striæ, but the species is not a particularly variable one.

As has been said, this is the *Nebria* which sometimes goes in collections as *columbiana* Casey. It belongs to the *ovipennis* group, but differs from *ovipennis*, its closest relative, in the submetallic lustre of the elytra and the much longer antennæ. It resembles also *Nebria kincaidi* Schwarz (*columbiana* Casey), but the latter is a more convex and brilliant species, with a more strikingly cordate prothorax, with the elytral intervals more interrupted, and with more prominent eyes. It was probably Casey's failure to point out the last character in comparison with *Nebria ovipennis* Lec. which first led to the misidentification of his species. *N. vandykei* is obviously distinct from the other American species of Nebria with obliterated humeri (*ingens* Horn, *spatulata* V. Dyke, *riversi* V. Dyke, and *lyelli* V. Dyke), although I know *riversi* and *lyelli* only from descriptions.

I take great pleasure in naming this Nebria for Dr. Edwin C. Van Dyke, who has discovered and described so many fine species of the genus in western North America.

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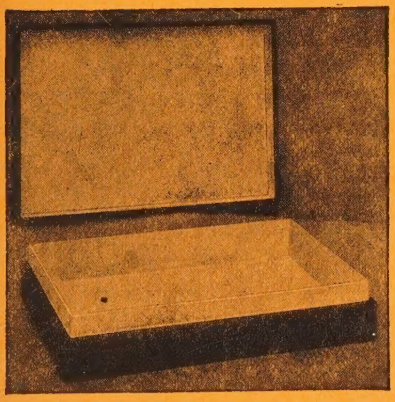

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